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THE EVOLUTION OF CULTIVATED CACAO

R. CIFERRI AND F. CIFERRI

Botanical Institute, Pavia, Italy

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INTRODUCTION

The senior author first undertook studies on cultivated cacao in the Dominican Republic and elsewhere in the Caribbean region 30 years ago. More recently, both of the writers were able to spend more than a year in Venezuela and Colombia, studying cacao in cultivation—with special reference to the best commercial grades—and investigating the remains of the old colonial cultures and the so-called "wild" cacao. Much detailed work remains to be done, but the results achieved so far are outlined in this report.

VENEZUELA, CENTER OF EVOLUTION OF THE BEST COMMERCIAL GRADES

First, it is necessary to consider why Venezuela (fig. 1) is the "key" to most problems connected with the evolution of the superior cacaos, the high quality Criollos and Forasteros.

The western part of Venezuela and a portion of Colombia constitute one of the two recognized pre-Columbian centers of cacao culture, the other being Central America and Mexico. In the former, where the history of cacao cultivation has been reviewed by Pittier (1924–1935) and Ciferri and Ciferri (1949–50), cacao cultivation has greatly increased and improved since the original half-culture; it progressed during the Spanish colonization, and today it includes the best cacao produced in Spanish America. The reasons for this continuous development seem to be that at least one of the two Criollos is probably indigenous to Venezuela, as is the peculiar Porcelain cacao and that the introduction or diffusion of an inferior Forestero some 50 years ago initiated hybridization which still continues. The cacao culture of Venezuela is a mosaic of more or less isolated populations extending from the southwestern and western extremities through the central regions to the extreme eastern and southeastern zones. It includes a wide selection of commercial cacaos, varying from those of inferior quality to some of the best in the world. The importance of Venezuela is that the evolution of its cacao population is still proceeding and that collections and observations made there are of the greatest value in throwing light on our problems.

An outstanding difficulty in the developmental study of cacao is the lack of reliable knowledge concerning the species of the genus *Theobroma,* especially regarding their distribution in a portion of Cen-

FIG. 1. Northern part of Venezuela including the cacao regions.

tral America and Mexico and in the enormous river basins of South America from the Orinoco Valley southwards to the lower Amazon basin, and from the Andes and the Pacific coast to the Atlantic. After the recent discoveries by Cuatrecasas (1944, 1952) of well characterized, previously undescribed species in a restricted area of western Colombia, it is apparent that our knowledge of the species of *Theobroma* is still very incomplete. Descriptions and specific keys (Ducke, 1925; 1940; Pittier, 1930; Chevalier, 1946) are very provisional so far.

Further, little is known about the cytology of the species. The first record of interspecific hybridization was that of Addison O'Neil and Miranda (1951). Also, data on the composition and characteristics of "wild" cacao populations are very scanty and fragmentary, e.g., the preliminary survey of Pound (1939) for Peruvian Amazonas; Stahel (1920) and Myers (1930) for Guyanas; a short report on eastern and southeastern Colombia (W.I.C.C., 1953); and a few older reports (summarized in Van Hall, 1932); in addition to our own surveys of Venezuela and Colombia.

Taxonomy and Nomenclature of Cultivated Species of Theobroma

Until the work of Pittier (1924) and Pittier and Chevalier (1925), the bulk of commercial cacao had been assigned, since the time of Linnaeus, to one species, *Theobroma cacao* L. *sensu lato*. Pittier revalidated an obsolete binomial of Bernouilli and distinguished *T. cacao* L. *sensu stricto,* corresponding to the Criollos cacaos, from *T. leiocarpa* Bern., based on an Amelonado cacao (a Forastero of inferior quality).

Pittier (cfr. 1932, 1935) emended the second species to include the lowest quality cacao (the Amazonian Calabacillo; Amazonian Forastero according to the nomenclature of Cheesman), thus distinguishing the Criollos (*T. cacao*) from the Calabacillo (*T. leiocarpa*).

This subdivision has been accepted by many students, including Cheesman (1932, 1938) who, however, later (Cheesman, 1944) criticized this classification, apparently on the basis of Pittier's 1925 paper (see the subsequent comment on Cheesman's views by Chevalier, 1944).

The present senior author has recognized one species and two subspecies in cultivated cacao (Ciferri, 1939–53):

T. cacao L. subsp. *typica* Cif. (1941, as variety) = *T. cacao* L. p.p. (sensu stricto) for the Criollos cacao, including the jordanon *T. sativa* (Lam.) Lignier et Le Bey var. *leucosperma* Chev. and *T. pentagona* Bern. which was accepted by Chevalier.

T. cacao L. subsp. *leiocarpum* (Bern.) Cif. (1933, as variety) = *T. cacao* L. p.p. for the Calabacillo cacao, including the jordanon *T. sativa* (Lam.) Lignier et Le Bey var. *melanosperma* and *T. sphaerocarpa* Chev.

The traditional, intraspecific division of cultivated cacao as summarized by Van Hall (1932), consolidated the two fundamental groups, Criollo and Forastero, the latter being subdivided into four subgroups: Angoleta, Cundeamor, Amelonado, Calabacillo.

Ciferri (1939) excluded Calabacillo (which has been referred to a subspecies as well as Criollos for the same reason), recognizing only the Forasteros, all derived from the cross *T. cacao* subsp. *typica* × subsp. *leiocarpa*.

The morphological characteristics are:

A. Maximum diameter of the pod greater than one-half of the length (typically elliptic or ovate to subspherical) .....Amelonado
AA. Maximum diameter of the pod less than one-half of the length (typically long ovate to long elliptical) .....B
B. Base of the pod more or less clearly narrowed; tip more or less acute (typically bottle-shaped) .....Cundeamor
BB. Base of the pod not narrowed, tip rounded to subacute (typically ogival) ...Angoleta

The morphology of many pods is intermediate between these categories and does not conform to any one group.

We agree completely with the criticism that these categories are not true taxa, but only morphological groups useful in describing cacao populations. For full details, see the monograph on cultivated cacao of the Dominican Republic by Ciferri (1933) and our surveys of Venezuelan and Colombian cacao.

Morphological Characteristics of the Pod

Pods have been classified on the following features in descending sequence of importance:

a) Shape (see above; also with intermediary categories).
b) Color of the shell just before ripeness: violet; mixed violet; red; mixed red; pink; mixed pink (pink on green stripes and green or pink shade): green and pale green with some intermediary shades.
c) Surface of the shell: tuberculate; rough; intermediate; smooth (rarely also reticulate).
d) Thickness of the shell: less than 15 mm; 16–20 mm; more than 20 mm.
e) Length: less than 15; 16–20; 21–25; more than 30 cm.
f) Longitudinal symmetry: symmetric or asymmetric
g) Tip: absent; rounded; acute; acuminate
h) Number of beans: less than 20; 21–25; 26–30; 31–35; 36–40; more than 40.

In a few instances other characteristics are employed e.g., the weight of fresh but ripe beans and in certain cases the height of the tree (very high; high; medium; low); productivity (very high; high; medium; low); type of branching, shape and length of old leaves.

Grading of the Beans

The variability in shape and size of fresh cacao beans is so great that it has not been possible to establish categories on the basis of these qualities. It is possible to recognize the large and long and as a rule more or less inflated (also a little irregular, frequently a little gibbose) beans of the Criollos cacaos, as opposed to those of the Calabacillo cacaos which are short and narrow, typically flattened or more or less inflated. The hybrid Forasteros contains all the intermediary categories.

Much more important is the grading of fresh beans in *fully mature pods*. The technique is fully explained in our paper (1954). For this evaluation a fully mature pod is opened, and the beans separated from the central rhachis; then each bean is cut with a stainless penknife and the color noted. The color of immature beans is always lighter, darken-ingurth increasing immaturity of the pod. Not all the beans of a pod are necessarily of the same grade. The average weighted mean is referred to as pod grading value (P.G.V.); n = the number of beans of each grade for the same pod; g = the respective grade:

$$\text{P.G.V.} = \frac{(n_1 \times g_1) + (n_2 \times g_2) + \cdots + (n_7 \times g_7)}{n}.$$

The standard has been selected after many years of research involving thousands of pods of phenotypically pure and hybrid cacaos. The classification comprises 7 groups, according to the following colors (nomenclature follows Ridgway, 1912):

No. 7.—Cotyledons almost white (cream-white and ivory white), rarely with very pale pinkish or mauve (lilac) shades, also in stripes or spots from white (ivory) or almost cream to pale olive-buff (XL: 21''' O–YY), rarely with indistinct shades of very light pink. True Criollo.

No. 6.—Cotyledons lilac to pinkish, as a rule, in the peripheral third; two-thirds of the central core whitish, but with stripes or shades of mauve or pink, periphery from pale rose purple to rose purple (XXVI: 67' V–R line f and line d), eventually with some shades of dull color to light lilac (same plate, line d); center as in No. 7. Commercial Criollo or "almost" Criollo.

No. 5.—Cotyledons lilac or mauve to very light violet on the two-thirds peripheral portion, and lighter to whitish in the central core, but with shades of pink

PLATE 1. Reproduction of the colored plate of M. S. Meriam (Amsterdam, 1705), the first iconography of Criollos Cacao in America (Dutch Guiana). The insertion of pods and flowers is fantastic, and the insects unrelated with cacao tree.

to mauve; periphery from pale lavender-violet to mauvette (XXV, line f, 61′ VR–V; 63′ R–V; 65′ RR–V); center as above, but also of the same, lighter shades. Superior Forastero.

No. 4.—Cotyledons dull-lilac or dull-mauve, at least in the peripheral two-thirds, and lighter (light-mauve to pink and also whitish) in the central core, as a rule not uniform in color; periphery Ontario violet to light hyssop violet (XXXVI, line b) or lavender-violet to Chinese-violet (XXV, line b); center lighter (Verbena violet to deep lavender, XXXVI, line d), or light lavender-violet to lilac (XXV, line d), but also periphery and center of the same shade. Average Forastero.

No. 3.—All the cotyledons purplish-violet, as a rule uniform but sometimes with a lighter, central core. From haematoxylin violet to petunia violet (XXV, line i), or from dull dark purple to dahlia carmine (XXVI, line k); center of the same shade or slightly lighter. Low Grade Forastero.

No. 2.—Cotyledons violet to dull-violet, rarely uniform; from anthracene violet to nigrosin violet (XXV, line k), rarely with some shades from dull dusty purple to dusky auricula purple (XXVI, line m, 67′ V–R and 69′, RV–R), as a rule uniform. "Almost Calabacillo (also very low grade Forastero?).

No. 1.—Cotyledons violet-black or black-purplish, as a rule uniform in shade; from dark anthracene violet to dark madder violet and dark nigrosin violet (XXV, line m) but always in the darkest shades, to dull dusky purple and dusky auricula purple (XXVI, line m, 67′ V–R and 69′ VR–V). True Calabacillo.

The No. 7 corresponds to subsp. *typica*, and No. 1 to subsp. *leiocarpa* of *T. cacao;* No. 6 to No. 2 are Forasteros, but No. 6 is very like the Criollos, while No. 2 is very like Calabacillo; No. 5, 4 and 3 are the average, commonest cacaos, recognized as commercial Forasteros of decreasing quality from No. 5 to No. 3.

Regions of Cacao Culture in Venezuela

The approximate distribution of the cacao regions of Venezuela is included in the geographical map (fig. 1) of the Northern Venezuela. From East (Atlantic coast) to West (adjacent to Colombia) they are:

1: *Delta of the Orinoco river* (officially *Delta Amacuro*) and the intermediate region of
2: *Caños de San Juan;*
3: *Peninsula of Paria* (officially Estado de *Sucre*);
4: *Barlovento* (officially Estado de *Miranda*), and, southward, 13: remains of the old cacao culture of *Orituco* (Estado de *Guarico*);
5: *Central Region* formed—from East to West—by the *Distrito Federal,* Estado de *Aragua* and Estado de *Carabobo;*
6: Estado de *Yaracuy;*
7: shores of the *Maracaibo* Gulf (officially Estado *Zulia*);
8–10: the three *Andine regions,* namely: 8: Estado de *Trujillo;* 9: Estado de *Merida;*
10: Estado de *Tachira;* 11: scattered cultures of *Arauca;* 12: *Meta,* both of the Estado *Apure.*
T: Trinidad (British West Indies).

The distribution of cacao populations is sketched in the fig. 2.

Cacao Populations of Venezuela

A few preliminary notes on the characteristics of the cacao populations of Venezuela, including the half (or "wild") culture or remains of old cultures, and the Cauca Valley in Colombia were published by the senior writer (1948, 1949) and by both authors (1949, 1950).

The notation of the fundamental types of cacao are: *Cr* = Criollos, *Ca* = Calabacillo; the hybrid Forastero are *Cr* × *Ca,* the increase of Criollos "blood" is indi-

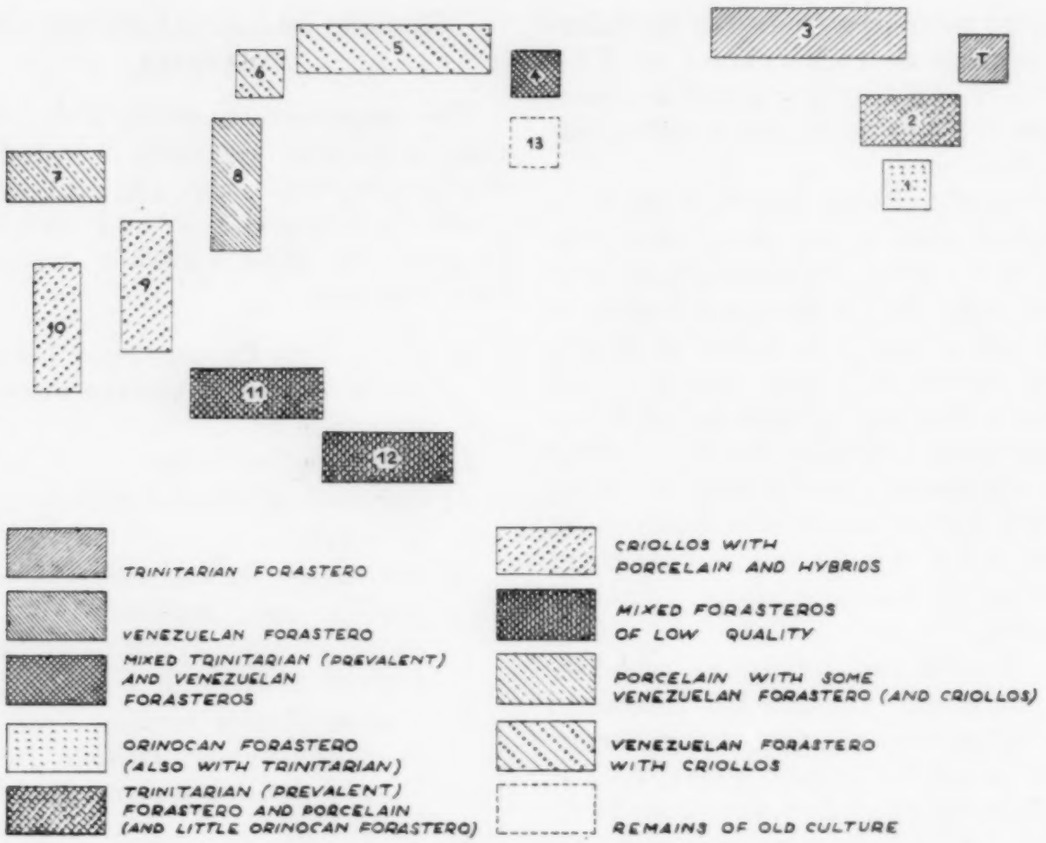


FIG. 2. Distribution of the fundamental cacao populations in Venezuela. (For the numbers corresponding to the regions of culture see the text.)

cated by the repetition of *Cr*. The seriation of the Forasteros is:

$$1.—(Cr \times Ca); \quad 2.—Cr(Cr \times Ca);$$
$$3.—Cr(Cr \times Ca)\ Cr.$$

VeCr = Venezuelan Criollo. *GrCr* = Green Criollo. Porcelain is marked *Po*.

Criollos.—Two Criollos are found in Venezuela: *a*) the locally named "Criollo de concha morada," "Criollo morado," "Morado colorado" or "Criollo de Venezuela," namely, "Violet Criollo" or "Venezuelan Criollo"; *b*) "Criollo verde" or "blanco," namely, "Green" or "Decolorized Criollo," from the color of the shell before maturity. The pod of both Criollos is of the same shape and size, with almost the same superficial texture, number and depth of furrows, and thickness; the beans are identical or almost so in shape, size, number and quality; habit, size and productiveness of the tree is also the same. The outstanding difference is in the color of the shell; that of Venezuelan or Violet Criollo is dull violet (but also with shades of carmine red color) before maturity, more or less covered by a thin layer of wax, and of the same color or slightly reddish when ripe.

The pod is a typical Cundeamor in shape, i.e., long, cylindrical, but with a narrowed, acuminate, as a rule more or less recurved distal end, with 5 deep furrows al-flattened basal end is also frequently slightly narrowed. The furrows are continuous from one to the other end of the pod.

The superficial texture of both Criollos is distinctly verrucose-tuberculate; in the Green Criollo the tubercles are smaller and more developed, but denser and almost conical, reaching to the deep furrow. In the Violet Criollo the tubercles are larger, shorter, sparser and more flattened; the deepest portion of the furrow is devoid of tubercles (or almost so). The basal end of Violet Criollo is slightly larger and flattened, and the apical end is

less acuminate and recurved and thinner than in the Green Criollo.

The furrows are identical or better developed in the Green Criollo. The thickness of the mature shell varies from less than 16 mm to more than 30 mm; about one half of the Violet Criollo fruits have a shell of 21–30 mm, and little less than half of those of Green Criollo are 16–20 mm.

The shape and size of Criollos beans are the same for both cultivars; they are large, flattened, ovoidal to elliptical, frequently with one end more rounded than the other.

The number of beans in each pod may be as high as 40, but 95 per cent of them contain from less than 20 to about 30 beans.

The weight of fresh, mature and unfermented beans per pod is very variable; in 70–80% of the pods examined, the total weight per pod ranged from 111 to 150 grams. Fresh bean must be graded No. 7, but the phenotypically pure Criollo is exceedingly rare, as also are the pods yielding mixed beans.

Genotypic Criollo also is exceedingly rare, being localized in a few small cultures or remains of old cultures in the Venezuelan Andes. The tree is large, longliving with large leaves, very susceptible to brown pod rot (*Phytophthora faberi*) and moderately susceptible to the watery-pod disease (*Monilia roreri*) and to witches broom (*Marasmius perniciosus*).

The beans suffer from a peculiar disease described as hearth rot (Ciferri, 1951). The etiology of this condition is obscure. It is not crytogamic. It may be nutritional or, more probably, the death of some beans in each pod may be caused by some heredity factor.

As do the best Forasteros, the Criollos suffer from deficiency diseases, more frequently than the inferior Forasteros.

Hybrids between Criollos.—Hybrids between both Criollos (*VeCr* × *GrCr*) are not easy to identify, being similar to the parents, sometimes to one more than the other. The best characteristic is the violet spotting light green of the immature shell pod; at maturity it is yellow, variously spotted with violet, purple or dull red. As a rule, the shell is greenish with more or less diffused shades of pink to carmine red, to entirely pinkish or very light carmine, with diffused greenish spots. The beans are the same as in both Criollos. Apparently *VeCr* with anthocianic pod shell is dominant over *GrCr*.

Porcelain.—The Porcelain cacao (*Po*), "Porcelano" or "Porcelana" in Spanish, is an unusual, localized and rare type. It is moderately frequent in region 7 and in the near by Colombia, but is also found in the diametrically opposed region 2 where it is very scarce.

This is an endemic cacao of Venezuela, apparently localized around the Gulf or Lake of Maracaibo. It is characterized by small pods, very similar in shape to Calabacillo, but also variable to a small Angoleta, shortly ovate, with rounded base and tip, surface very smooth and brilliant, without furrows or with 5 very superficial furrows; shell thin (less than 5 mm thick), but hard and easy to break, dull to pale-green and also whitish-green before maturity; yellow when ripe.

The seeds are abundant, as in Calabacillo, and flat to half-rounded or asymmetric, very small, sweet, cinnamon to light-brown when fermented, but lacking the agreeable smell when roasted peculiar to the Criollos cacaos.

The cotyledons are white to slightly yellowish (cream), never pink or pink-shaded as in the typical Criollos. These characteristics are those of phenotypically pure cacao because in most cases the Calabacillo is hybridized with other cacaos. The tree gives an average yield higher than that of Criollos but less than low-grade Amazonian Forastero, in spite of the small beans.

The pod is very susceptible to watery pod disease in region 7; apparently this disease spread in the Venezuelan Andes up to Yaracuy from this region. It is

also susceptible to witches broom as in region 2.

The origin of the Porcelain is unknown. We suspect that it is a leuco-mutation of some Calabacillo or some Amazonian Forastero of low quality, approaching Calabacillo. All the characteristics of the pod and the bean are very near Calabacillo but the beans are entirely white and sweet, being devoid of anthocianins, and lack the fine aroma characteristic of fermented and roasted Criollos. Our hypothesis is based not only on the morphological similarity of Porcelain and Calabacillo pods but also on the high sensitivity to the cryptogamic diseases, which are considered of Amazonian origin. On the other hand, a white-seeded mutation of Brazilian cacao has been described by Miranda and Silva (1939).

In spite of the decrease in commercial importance of this cacao during the last 50 years, the mixed cacao from Maracaibo, containing a high percentage of Porcelain, Criollos and Venezuelan Forastero, is highly esteemed in world markets.

Hybrids between Criollos and Porcelain (Criollain).—Both hybrids (*VeCr* × *Po* and *GrCr* × *Po*) are found in region 7, but rarely. The grade is also 7, but with mixed white and white with slight pink shades, and aromatic. The beans are of any intermediate size and shape between those of the parents, from slightly less of Criollos to a little larger of Porcelain, but also large and plump to small and flat. The pod is larger than in Porcelain but smaller than in Criollos, with shades of carmine-red to purplish for (*VeCr* × *Po*) or green for (*GrCr* × *Po*). Of course, the hybrid *VeCr* × *Po* is more easily recognized than is *GrCr* × *Po*.

An elegant problem is posed by the nomenclature of these hybrids in regard to the typical Forasteros. Due to lack of knowledge on the origin of Porcelain, they cannot be considered as true Forasteros, and we propose the term "Criollain" (in Spanish "Criollano") coined from the words Crioll[o] and [Porcel]ain.

It is possible that in regions 7, 8 and 9 the more complex hybrids, *Po*(*VeCr* × *GrCr*), and in region 7 only also *Po* × *Cr* (*Cr* × *Ca*)*Cr* are present but unrecognizable without thorough analysis.

Forastero hybrids: Amazonian Forastero.—Although true Calabacillo (*Ca*), with the beans graded 1, has never been found in Venezuela, we have observed a number of pods of grades 1 and 2, chiefly in region 4 (fig. 3).

The pods of this "almost" Calabacillo are green or pale green, yellow or yellowish when ripe; small, of a short and rounded Amelonado shape, with a thin but hard, woody shell. As a rule, diffuse or localized light shades of red on the shell, even on the very superficial ridges, but this is not a sign of superior "blood," as Cheesman (1944) considered for similar pods found by Pound (1939) in the Amazonian Valley approaching Colombia that is, on the border of the original area of Amazonian cacao. The same, or an allied, cacao has been described by Ducke (1925) in northern Brasil. The most recent finding is that of the Trinitarian expedition to western Colombia (W.I.C.C., 1953). There is not yet any adequate description of the authentic Calabacillo because it has not been analyzed in detail. The beans are small, very flat and very bitter, fermentating slowly.

Notwithstanding, it is convenient for our purpose to treat both Calabacillo and the complex called Amazonian Forastero by Cheesman under the symbol *Ca*.

Forastero hybrids: Orinocan Forastero.—In our definition, Orinocan Forastero, is *Cr* × *Ca*, intermediate between Amazonian (*Ca*) and *Trinitarian* [*Cr*(*Cr* × *Ca*)] Forasteros. It is frequently found at the mouth of the Orinoco (region 1), in mixed culture with Amazonian (or near Amazonian) and Trinitarian Forasteros. Less frequently it occurs also in scattered cultures in regions 11 and 12, first appearing in the Median Orinoco and on the opposite Colombian side. It is not uncommon in region 4, but rare in 3.

It is a tree of medium productivity,

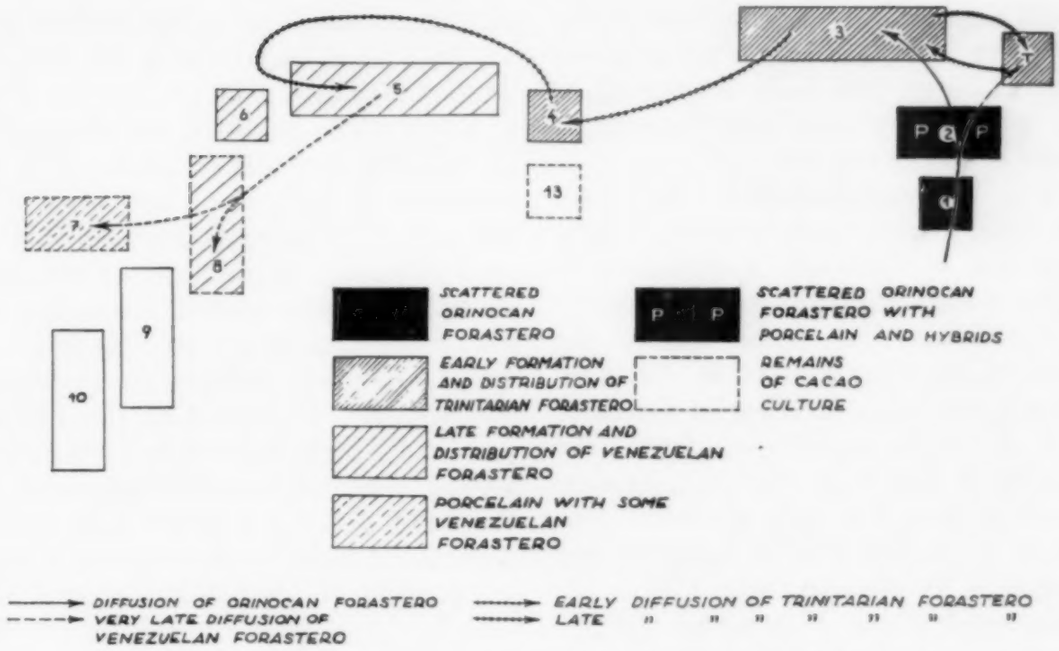

SCATTERED ORINOCAN FORASTERO
SCATTERED ORINOCAN FORASTERO WITH PORCELAIN AND HYBRIDS
EARLY FORMATION AND DISTRIBUTION OF TRINITARIAN FORASTERO
REMAINS OF CACAO CULTURE
LATE FORMATION AND DISTRIBUTION OF VENEZUELAN FORASTERO
PORCELAIN WITH SOME VENEZUELAN FORASTERO
DIFFUSION OF ORINOCAN FORASTERO
VERY LATE DIFFUSION OF VENEZUELAN FORASTERO
EARLY DIFFUSION OF TRINITARIAN FORASTERO
LATE " " " " " " "

FIG. 3. Diffusion of the Forasteros (and other cacaos) in Venezuela.

with relatively small pods, as a rule of Amelonado shape, slightly enlarged, but intermediate between Amelonado and Angoleta; the shell is variable but smooth or almost so, as a rule with 5 to 10 not well defined furrows; immature pods are green with carmine to violaceous patches, but also more or less uniformly red, ripe yellow with red to purplish shades, with hard but not, or not very, woody shell; beans small, bitter; as a rule grade 3, sometimes also grade 2 (fig. 3).

Forastero hybrids: Trinitarian Forastero.—This is the classical Trinitarian cacao $[Cr(Cr \times Ca)]$, the well known Forastero which has often been described from Trinidad and elsewhere (see Pound, 1932, 1933). It is also the commonest good, but not a superior Forastero, extending from Trinidad to the Dominican and Haiti Republics, up to Mexico and Central America, on the American it has a mainland spread from the Guyanas to Brasil and from Colombia at least to Ecuador. In Venezuela it is frequent in region 1, 2, 3 and 4 but rare elsewhere.

The characteristics are well known. The beans are typically grade 4. The origin and early spread of this cacao has been discussed by Ciferri (1949). He found that the first colored illustration of Green Criollo was published by the Dutch engraver M. S. Merian (1805) reproduced (in black) in plate I. Thus by the beginning of the XVIII century, a Criollo had spread from Dutch Guyana to Trinidad and elsewhere. After the "blast" (the nature of which is in dispute) which in the year 1727 virtually destroyed the Criollo plantations in Trinidad, a hardier type of cacao was introduced into that island.

Cheesman (1944) was the last to suppose an introduction from eastern Venezuela; but it is now well established that in Venezuela, up to the year 1825, only the two Criollos were widely cultivated, with the possible exception of the Paria Peninsula (region 3). In this Estado Sucre we found a very mixed cacao population, more than in any other Venezuelan region of cacao culture. To sum up, this population is distinct from both the Trinitarian and the Venezuelan Forasteros, in spite of possible, later reintròduction of both Forasteros in the same region.

That the hardier cacao introduced into Trinidad would be obtained from the most meridional cacao zones from the mouth of the Orinoco to the Guyanas, seems less

probable than an introduction from Paria, a few miles from Trinidad. In addition, culture of cacao was fully developed in Paria, while it was poor and scattered in the very southern regions.

In this Venezuelan region 3 the most widespread cacao is derived from an early introduction of Orinocan Forastero (*Cr* × *Ca*), crossed with pre-existing strains of the Criollos. In other words, the Trinitarian cacao, originated in the Paria Peninsula (and now Trinitarian Cacao of Paria) is indistinguishable from the Trinitario of Trinidad. In past decades, more than now, the bulk of cacao produced in Paria was sold in Trinidad and marketed as Trinitarian cacao (fig. 3).

Forastero hybrids: Venezuelano.—This cacao [*Cr*(*Cr* × *Ca*)*Cr*] is the best South American Forastero, nearer to the Criollos than any other. It has been fully described by the present writers (1949, 1950, 1952).

This Forastero is cultivated in regions 5, 6 and 8, but commercial quantities are produced only in region 5, marketed mostly as "Caracas" or "Puerto Cabello" cacao. It is rare elsewhere but is found also in region 7 up to the Andine zones. It has also been found in Colombia (Cauca Valley).

The typical grade of this Forastero is 5, reaching (and mixed) to 6. It is characterized by large pods, but smaller than those of the phenotypic Crillos. They are as a rule long, asymmetric or symmetric, of an atypic Cundeamor shape, but variable from Cundeamor to Angoleta. The surface is mostly tuberculate or rough to half-rough. The color of the immature pod is variable according to the Criollo parent: violet-red to blood-red, with green longitudinal striae or green spots from the Venezuelan Criollo; light-green or yellowish-green with pinkish shade from Green Criollo. The trees are medium to large, of medium to very high productivity (for details see Ciferri, 1949) (fig. 3).

Evolution of the Cacao Populations in Venezuela

To sum up, the fundamental types of cacao hybrid between the subsp. *typica* (Criollos) and the subsp. *leiocarpa* (Calabacillo) are as follows:

Calabacillo [*Ca*] or Amazonian Forastero

×

Criollos [*Cr*] = Orinocan Forastero [*Cr* × *Ca*]

×

Criollos = Trinitarian Forastero [*Cr*(*Cr* × *Ca*)]

×

Criollos = Venezuelan Forastero [*Cr*(*Cr* × *Ca*)*Cr*]

The distribution of the aboriginal cacao (fig. 4) covers a septentrional area with the so called Central-American Criollo and a meridional area of both South American Criollos. The affinity of the Central-American Criollo, which is not discussed here, has not been fully analyzed; it appears to be derived from a

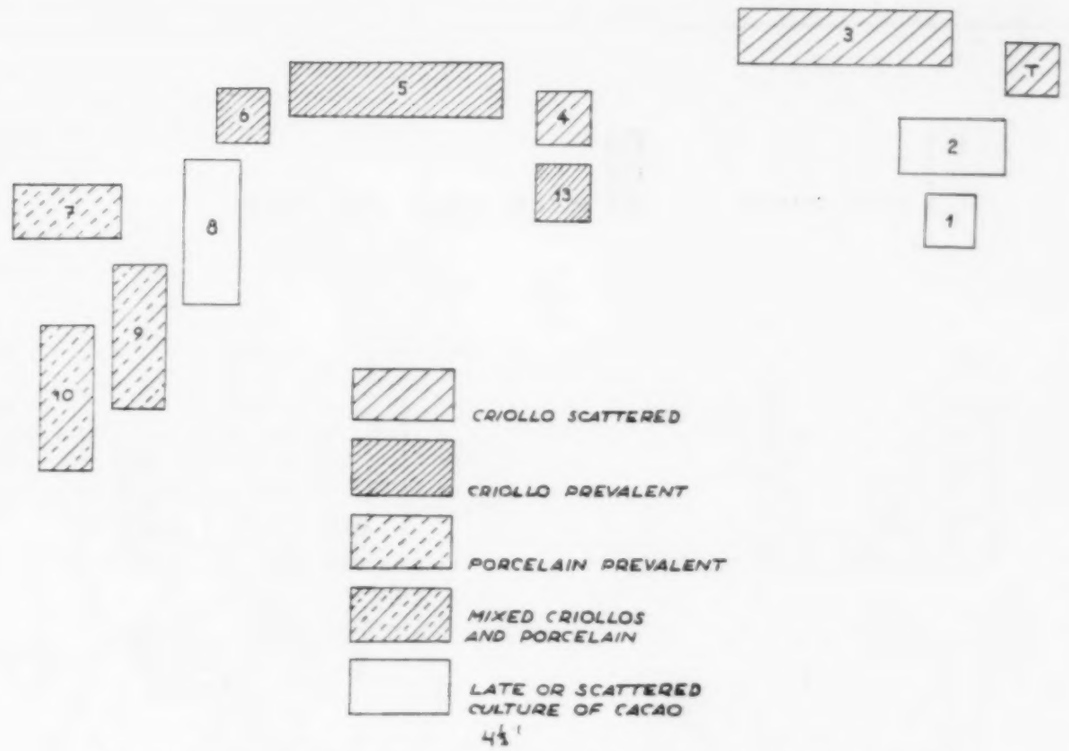


FIG. 4. Early distribution of Criollos and Porcelain cacaos in Venezuela.

cross between both Criollos (*Ve Cr* × *Gr Cr*).

In continental South America the area of the Green Criollo is much greater than that of the Venezuelan Criollo; the same applies to Venezuela. The derivation of one from another is still obscure. It would be easy to suppose that the Green Criollo is derived from the anthocyanic Criollo by an albino mutation, as was Porcelain from Calabacillo. As the Green Criollo is a little hardier than the Ven-

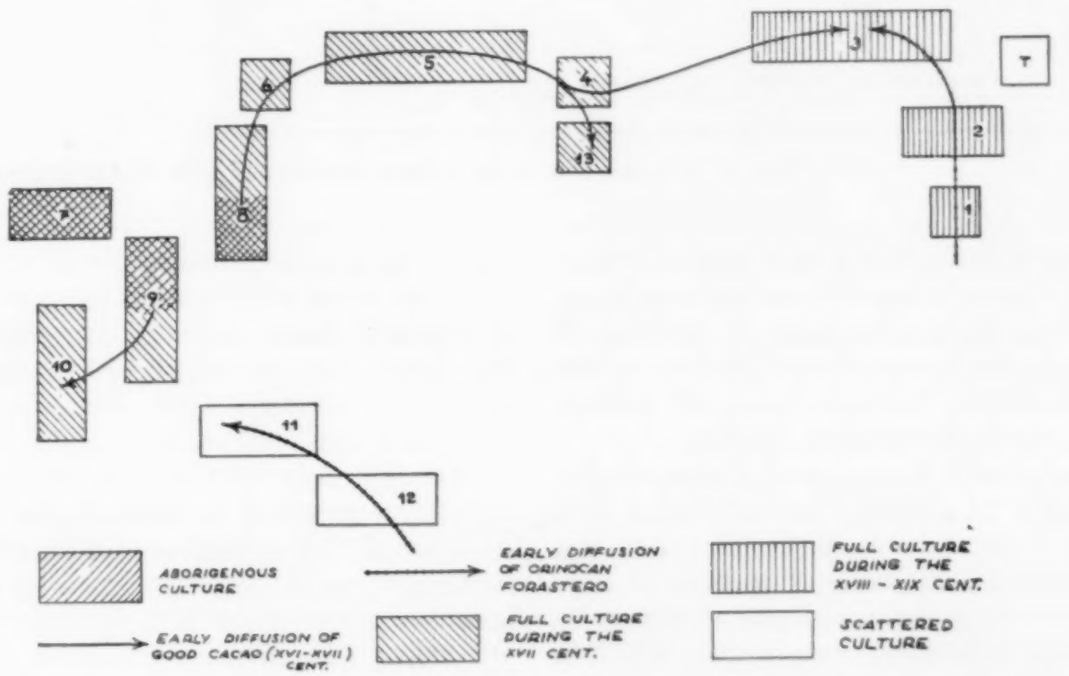


FIG. 5. The cacao culture in Venezuela from the aborigenous cultivation up to the XIX century, with the fundamental ways of diffusion.

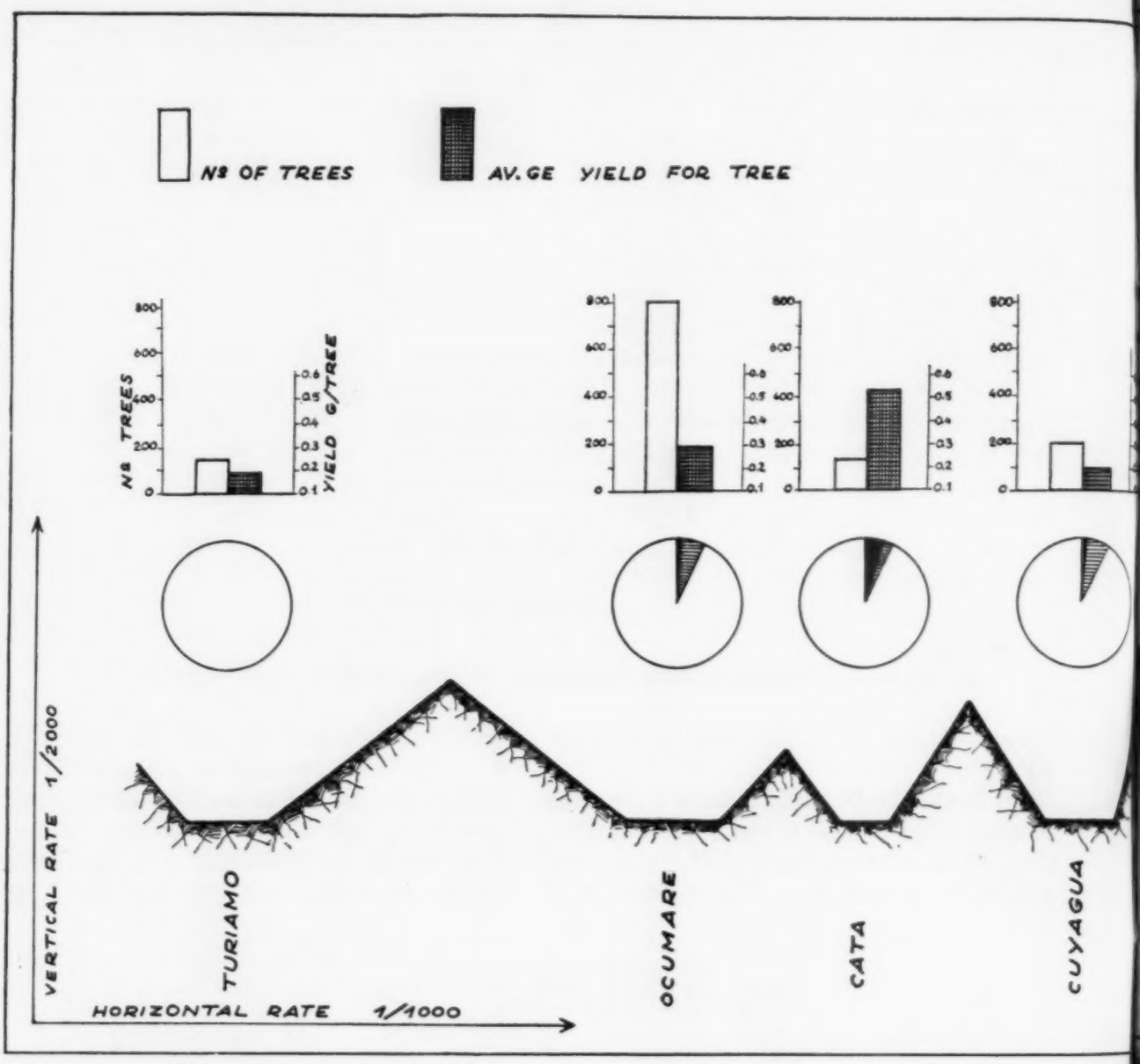
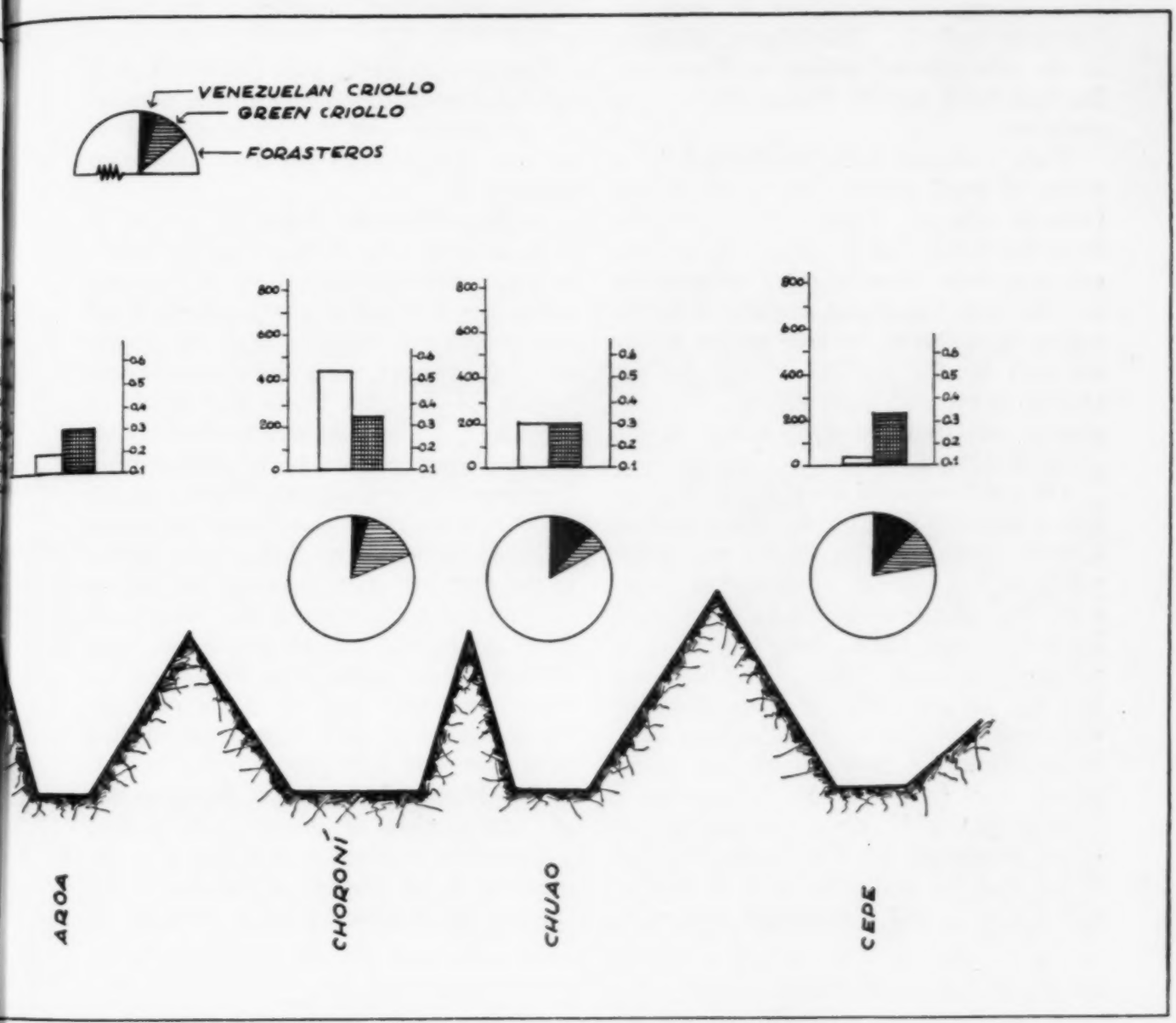


FIG. 6. Composition of the culture, numbers of trees and average yield of the ca

ezuelan Criollo, and a little more resistant to unfavorable environmental conditions and possibly to cryptogamic diseases, it may be supposed that diffusion of the Green Criollo has been easier and greater than of the Venezuelan Criollo.

In figure 3 the original presumed distribution of Criollos is sketched. The natural cross between Criollos and the meridional Amazonian Forastero is supposed to have occurred in the region overlapping both areas, namely, the valley to the west of the Amazon, from Rio Negro and Rio Branco up to the Orinoco. This great region is almost unexplored, at least from our point of view; but the presence of Orinocan Forastero from the mouth of the Orinoco to the scattered cultures at east of the Orinoco (Rio Meta-Rio Caroni) is a confirmation of this idea.

Probably until the XVII century, this Forastero remained localized in the area, or diffused slowly as small and scattered indigenous cultures to the Orinoco Delta, later being introduced into the intermediary region of Caños de San Juan up to the Paria Peninsula. The Delta Amacuro culture had been fully established by



ltivations in the seriate valleys of the Distrito Central (State of Aragua), Venezuela.

the XIX century with several strains superimposed on the pre-existing Orinocan Forastero, then crossed with it.

Presumably, the cross between the Orinocan Forastero and the previously diffused Criollos originating the Trinitarian Forastero, occurred independently in several cacao regions from the Guyanas to the Centro-Oriental Venezuela, east of the boundary of Caracas-La Guaira cultures that remained free from hybridization. The multiple back-crosses made in this great area on scattered cultures gave rise to local cacao populations. In Venezuela two places are now easily recognizable, the center of the Paria Peninsula (region 3) and the Barlovento region (region 4), the later producing the bulk of the Venezuelan cacao of the lowest quality.

The evolution of cacao populations together with the progress of cacao culture in Venezuela to the beginning of the XIX century, is evident from figure 5.

The evolution of the cacao populations in the central and western regions of Venezuela is much more evident as hybridization occurred during the past century

(central region) or is yet in progress (western region). The history of cacao in the post-colonial period in Venezuela has been dealt with by Pittier (1932) and ourselves.

These cultures were established in a series of small parallel but more or less isolated valleys. They were developed from the XVII century chiefly by monks, escaping from Spanish royal domination, and the free but illegal markets were favored by isolation, by free access to the sea and by the asylum offered by the church to escaped black slaves. The region is composed by eight valleys in the State of Aragua.

The localization of the cultures in Aragua is sketched in figure 6. Until the last century, only Criollos cacao was cultivated in this region. Trinitarian Forastero has been introduced, probably from Barlovento or Paria, into the extreme western Turiamo Valley. The Trinitarian has slowly diffused from Turiamo eastward, and the progress is now fully recognizable by analysis of the cacao populations (see fig. 6). The cross of Trinitarian with pre-existing Criollos cacao originated the Venezuelan Criollo, in populations oscillating from an almost-Criollos to a full Trinitarian, according to the nature and intensity of the back-crosses.

The percentage of both Criollos and of the Forasteros, together with the number of cacao trees and the average yield of dry fermented cacao per tree, is shown in figure 6.

In the Carabobo State (5, West of Aragua State) the Trinitarian Forastero is scarce and scattered, but, on the contrary, it is frequent in the poorly diffused cacao culture of Yaracuy State (6, Southwest of Aragua), as in the poorest cacao culture of Trujillo State (7, South of Yaracuy). The evidence is that Trinitarian Forastero has been spread from Yaracuy to the East, the West and the South. Yaracuy was an important centre of cacao culture from late colonial times to the first half of the century, as well as an important commercial for cacao and other products. It is supposed that from Yaracuy some Venezuelan Forastero has been introduced into the State of Zulia (Maracaybo, 7) and that hybridization with Porcelain is in progress.

The Maracaybo region is the boundary of introduction of Venezuelan and/or Trinitarian Forastero southwards, because it is not present in the cacao cultures of the Andine States of Merida (9)

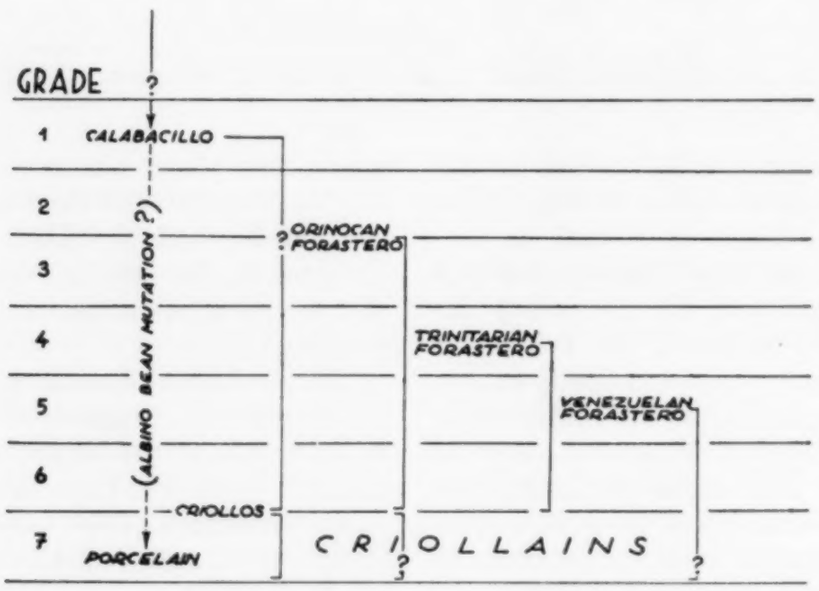


FIG. 7. Interrelationship between basic types of cacao and hybrids with the grading of fresh beans.

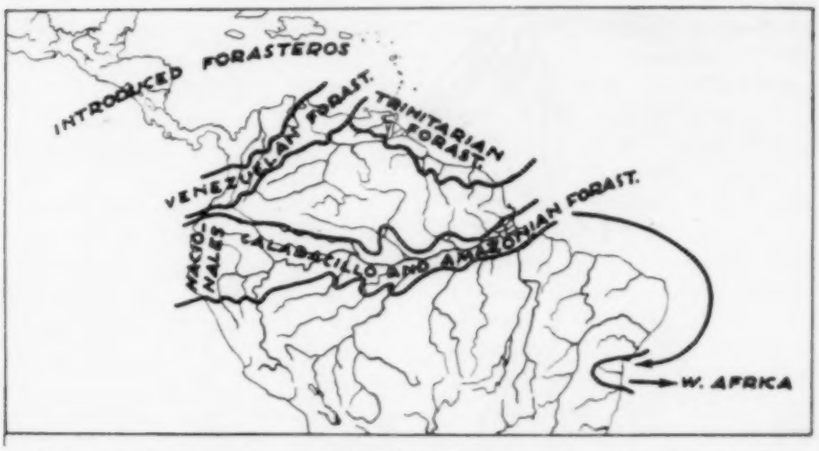


FIG. 8. Presumed general diffusion in South America of the Forasteros.

and Tachira (10). Here only Criollos (rarely Porcelain and Criollos hybrids) are found in culture or in the scattered remains of the old cultures. These and other data are summarized in figure 3. In fig. 7 the interrelationship between basic cacao types and hybrids with grading of fresh beans is sketched.

THE AMAZONIAN FORASTERO AND THE WEST AFRICAN CALABACILLO

The approximate distribution of Amazonian Forastero in continental South America is sketched in figure 8. In Ecuador, according to a few scattered data, there are mixed populations of several Forasteros and more or less autochthonous populations. The increasing culture of Brasilian cacao in the State of Bahia is fundamentally that of Amazonian cacao, but with a notable range of variability and some segregates (Bondar, 1929). The presumed early aborigenous cacaos and the introduction before the 20th century are summarized in the figures 9 and 10.

It is generally admitted that the greater cacao output of the world—that of West Africa, chiefly Gold Coast—was derived from a very few Brasilian strains, via San Tomé and Principe Islands. This exceedingly narrow base of origin has led to an extraordinary uniformity in the habitat of the trees and in their pods and beans. The quality is extremely low, especially in types 1 and 2. The most aberrant pod shape is that described by Chevalier as the small African species *T. sphaerocarpa,* apparently a segregate from the Amazonian Forastero. The most likely antecedent of Calabacillo is this

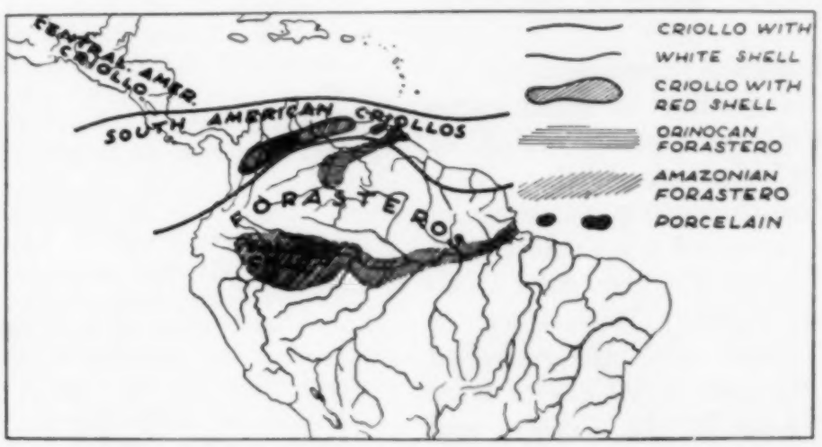


FIG. 9. Presumed early distribution of aborigenous cacaos in South America.

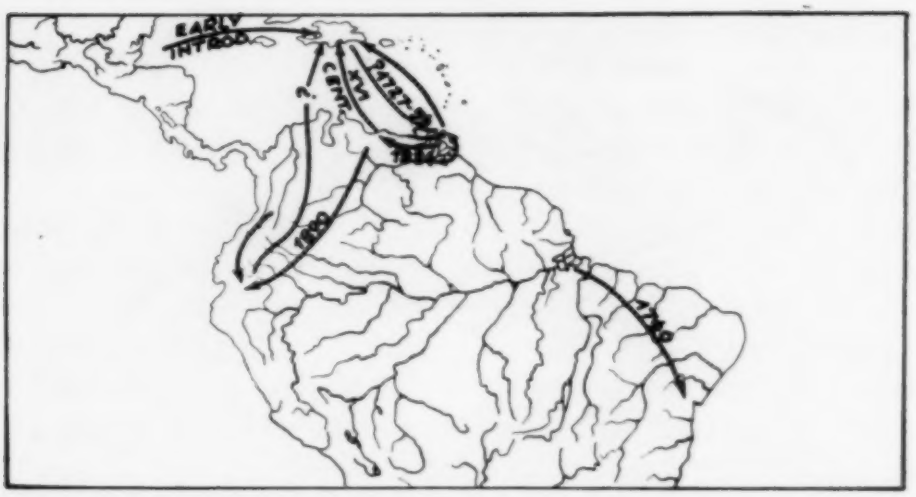


FIG. 10. Some introduction of cacao groups prior the XX century.

spherical, small-podded cacao with bitter and small beans.

In conclusion, a more detailed exploration of wild and semi-cultivated cacao populations of South America is needed, together with a better knowledge of South American wild species of their affinity and their geographical distribution. Such a survey would be of great interest not only for the improvement of cacao, but also for prevention of the serious endemic crytogamic South American diseases witches broom and watery pod and of virus diseases, such as African swollen shot.

SUMMARY

The outstanding position of the Republic of Venezuela, as center of evolution of the best commercial cacaos, is emphasized. The taxonomy of the species of the genus *Theobroma* is briefly discussed, together with the systematic status of cultivated cacaos.

The morphological characteristics of cacao pods and grading of fresh cacao beans are summarized and the regions of cacao culture in Venezuela listed.

The evolution of cacao populations of Venezuela are discussed from the poorest (Amazonian Forastero), very near Calabacillo, to the highest (Red-shelled or Venezuelan Criollo and Green-shelled Criollo). In the past only Criollos were cultivated, at least in the Central and Western regions of Venezuela. The Amazonian Cacao has been introduced or diffused, and crossed with Criollos so that this speciation of cacao, marked by an increase of Criollo "blood" is now evident: Orinocan Forasteros, Trinitarian Forastero and Venezuelan Forastero.

In addition, Porcelain cacao (supposed to be an albino mutant of Amazonian Forastero or Calabacillo) and Porcelain × Criollos hybrids ("Criollain") are discussed.

The actual evolution in the cacao population is deduced from the culture of the Central sector to the Andine regions.

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PLEIOTROPY, NATURAL SELECTION, AND THE EVOLUTION OF SENESCENCE [1]

GEORGE C. WILLIAMS

Michigan State University

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Senescence is a widespread phenomenon, but it has been largely neglected by non-medical biologists. This neglect may be attributed to a number of causes. One is that the process seldom presents itself to students of natural populations, since recognizably senile individuals are not often found in the wild. Another, perhaps, is an emotional difficulty associated with aging, a situation that was hardly helped by the early clinical association of senescence with sex hormones. Another is the existence of theories that have gained tacit acceptance, despite their conceptual obsolescence and poverty of factual support. The most injurious of these is the identification of senescence with the "wearing out" that is shown by human artifacts. A moment of serious consideration should convince a biologist of the fundamental dissimilarity between these two processes. The breakdown of human artifacts is strictly mechanical and is readily cured by mechanical repairs. The system is a static one, since the same material is continuously present, and there is no endogenous change with the passage of time. An organism, on the other hand, is an open system in a state of material flux. Even such structures as bones maintain constant exchanges with the environment. Moreover, an organism produces itself by a morphogenetic process. It is indeed remarkable that after a seemingly miraculous feat of morphogenesis a complex metazoan should be unable to perform the much simpler task of merely maintaining what is already formed.

It is true, of course, that some parts of organisms do literally wear out. Human teeth, for instance, show wear similar to that of any tool subjected to friction, but this wear is no more a part of senescence than is the wearing away of replaceable epidermal cells. The senescence of human teeth consists not of their wearing out but of their lack of replacement when worn out.

August Weismann (1891) was the first biologist of the evolutionary era to advance a theory of senescence. He believed that organisms must inevitably show a decline analogous to that of mechanical devices, but that, in addition, there was a specific death-mechanism designed by natural selection to eliminate the old, and therefore wornout, members of a population. He did not clearly indicate how such a mechanism could be produced by natural selection. He was likewise dubious about the exact nature of the death-mechanism, but indicated that it might involve a specific limitation on the number of divisions that somatic cells might undergo.

Weismann's theory is subject to a number of criticisms, the most forceful of which are: 1) The fallacy of identifying senescence with mechanical wear, 2) the extreme rarity, in natural populations, of individuals that would be old enough to die of the postulated death-mechanism, 3) the failure of several decades of gerontological research to uncover any death-mechanism, and 4) the difficulties involved in visualizing how such a feature could be produced by natural selection.

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Point number one was discussed in the opening paragraph, and points two and three will be documented in connection with my own theory. Point number four is concerned with the obvious conclusion that, other things being equal, a long-lived individual will leave more offspring than a short-lived one. If there is no specific death-mechanism, it is just as obvious that an individual that deteriorates slowly would be favored over one that deteriorates rapidly. Natural selection should ordinarily proceed towards lengthening life, not shortening it. Such selection, at the individual level, could conceivably be countered by selection at the population level, if senescence somehow favored group-survival. This suggestion was made by Allee *et al.* (1949: 692). The efficacy of such selection depends upon a rather complicated series of assumptions with respect to population sizes, degree of isolation, and relative strengths of the selective forces (Wright, 1945). A theory based on the simpler and more widely applicable principle of selection within a group would be preferable, unless the assumption of effective between-group selection proves to be necessary.

The neglect of senescence by modern biologists has not, of course, been absolute. Recent years have seen the publication of a number of reviews, the most valuable of which are those of Comfort (1954, 1956). Also there is an increasing awareness of the decline of selection pressures with increasing age. This principle, a central part of the theory developed here, is first recognizable in the work of Bidder (1932), and has since been stated or implied by Haldane (1941), Medawar (1953), and Comfort (1956). The principle is implicit in the currently recognized definition of a lethal gene as one that results in death before the reproductive period. However, the relationship of age to selection has never been precisely formulated.

Comfort is severely critical of Weismann's theory, and offers in its place the theory that senescence is selectively irrelevant. He argues (e.g., 1956: 39) that senescence is outside the developmental program that concerns natural selection, since almost no wild organisms ever attain the senile stage. I believe that this theory is incorrect. Its fallacy lies in the confusion of the process of senescence with the state of senility, and in an inaccurate conception of the relationship of age to selection pressures. No one would consider a man in his thirties senile, yet, according to athletic records and life tables, senescence is rampant during this decade. Surely this part of the human life-cycle concerns natural selection. The rate of senescence, as measured by life tables, is known to be subject to genetic variation (Gonzales, 1923; Kallman and Sanders, 1948). It is inconceivable in modern evolutionary theory that senescence, such as operates in man between ages thirty and forty, is selectively irrelevant.

I shall assume initially, therefore, that senescence is an unfavorable character, and that its development is opposed by selection. To account for its prevalence, therefore, it is necessary to postulate another force that favors its development in such a way that the observed variations in senescence reflect variations in the balance between these two forces. I believe that this other force is an indirect effect of selection, and results from the selection of genes that have different effects on fitness at different ages.

A number of workers have postulated that senescence might result from processes that are favorable early in life but have cumulative bad effects later on. Medawar (1953) expressed this concept in genetic terms by suggesting that linkage and pleiotropy might be involved in keeping favorable and unfavorable traits together, but he failed to elaborate on either possibility. Pleiotropy plays an essential role in the theory developed in this paper, but not linkage. Linkage might keep traits together for a time in a single line of descent, but I fail to see how it could contribute to the develop-

ment of senescence in a population as a whole unless crossover values were infinitesimal. Such a condition would approach pleiotropy and no special theory based on linkage need be elaborated.

The Theory

Four factors are initially assumed:

(1) A soma that is essential to reproductive success but no part of which is passed on in either sexual or asexual reproduction.

(2) Natural selection of alternative alleles in a population.

(3) Pleiotropic genes of a special sort. It is necessary to postulate genes that have opposite effects on fitness at different ages, or, more accurately, in different *somatic environments.*

Convincing examples are hard to find, because we seldom know the total survival value of a gene in a wild population, let alone its values in different parts of the life cycle. The best examples I can offer are at the *black* and *speck* loci in *Drosophila melanogaster.* Most laboratory mutants decrease longevity, but these two increase it, at least in the males under laboratory conditions (Gonzales, 1923). *Black* and *speck* are rare in nature, despite their beneficial effect on vigor late in life. The wild alleles of these genes must confer some earlier advantage that offsets the later disadvantage. Other possible examples exist. Caspari (1952) lists a number of genes of Drosophila and the moth Ephestia that have conspicuous effects on adult characters and also alter the rate of development. Bridges and Brehme (1944) list a number of mutants of *Drosophila melanogaster* that are named for conspicuous effects on the adult but which also alter the larval phenotype in some way. Examples are *glass* and *sparkling,* which alter the size, shape and texture of the eye in the adult and the color of the malpighian tubules in the larva. Quite conceivably these different effects at different times could have opposite influences on survival. However, there seems to be little necessity for documenting the existence of the necessary genes. Pleiotropy in some form is universally recognized, and no one has ever suggested that all the effects of a gene need be equally beneficial or harmful, or that they must all be manifest at the same time.

(4) Decreasing probability of reproduction with increasing adult age. An individual entering a population has a *reproductive probability distribution* (fig. 1, solid curve). For an organism such as

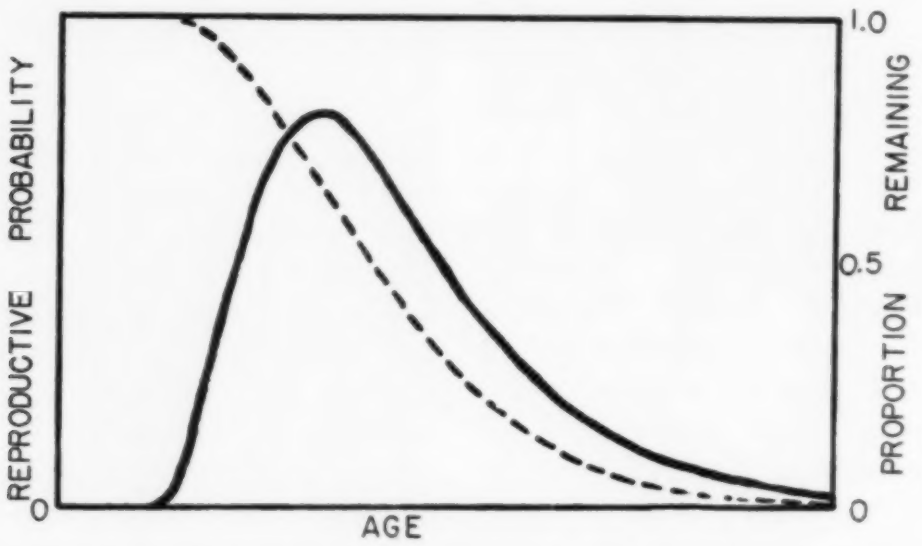

Fig. 1. Relationship of age to probability of reproduction. The solid curve is the reproductive probability distribution. The dashed curve indicates the proportion of the total probability that remains after any given age.

man, who has no definite breeding season, there would be a rise from zero just befor sexual maturity to a peak value shortly thereafter. Then there would be a decline due to a number of factors in man, among them senescence. But even in the complete absence of senescence there would always be a cumulative probability of death. This would produce a decline in reproductive probability, because the probability of reproduction at any age is a function of the probability of surviving to that age. No matter how low the mortality rate there is always a greater chance of surviving to age A than to age $A + 1$.

The fourth assumption need not imply that an individual of age A has a greater likelihood of reproducing itself than an individual of age $A + 1$. If an individual has, in fact, survived to age $A + 1$, the factor of probability does not apply. Medawar (1955) has proposed a mathematical formulation of the reproductive potential of an individual of a certain age in a species characterized by senescence. It was proposed as a measure of the extent of senescence at that age. The fourth assumption relates only to zygotes, and does not imply that senescence is operative.

The reproductive probability distribution of a seasonal breeder would have not one but a series of modes, one for each breeding season. Once maximum fecundity has been reached, however, each successive peak would be lower than the preceding one, due to the probability of death between the two seasons.

Wright (1956) has proposed the following model of the natural selection of a gene with mixed effects on fitness:

$$(1) \quad W = (1 + S_1)(1 + S_2) \ldots (1 + S_n)$$

where W is the selection coefficient of a gene and S_1, S_2, etc. are the advantages or disadvantages associated with its separate effects. Such selective effects consist of two factors. One is the direction and magnitude of the effect itself. The other is the proportion of the total reproductive probability influenced by the effect. This second factor would depend upon the amount of time during which the influence operates, but the relationship would not be a simple proportionality with time. The reproductive probability per unit time in the affected period would also be important.

Equation (1) can therefore be restated as:

$$(2) \quad W = (1 + m_1 p_1)(1 + m_2 p_2) \ldots (1 + m_n p_n)$$

where m is the magnitude of an effect and p is the relevant proportion of the reproductive probability. Obviously a gene that conveyed a slight increase in fitness with a high p-value might be favorably selected in spite of a serious decrease in fitness with a low p-value. This, I believe, is the key to understanding the evolution of senescence, because any genic effect that arises late in life will have a low p-value. Natural selection may be said to be biased in favor of youth over old age whenever a conflict of interests arises. Medawar (1952) reached precisely this conclusion by a somewhat different line of reasoning.

If a genic effect influences the survival of the soma in any way, it will alter the value of the entire reproductive probability that follows the onset of the effect. This is true even if the effect is expressed for only a short period. An influence on the likelihood of coming successfully through the birth process would be an example. It would alter the probability of survival to any age subsequent to birth, and therefore of reproduction at any age subsequent to birth. For such an effect, coming at any time before the reproductive period, the value of p would be unity. Altering the order of such effects would alter the order but not the values of the factors to be multiplied in equation (1) and this would have no influence on the product.

An effect on survival coming during the adult period, however, would alter only

that part of the reproductive probability that follows the age of onset (dashed curve in fig. 1). This proportion, the maximum value of p for any given age, is therefore a measure of the selective importance of that age. Since p starts to decline at the age of reproductive maturation, this point should theoretically mark the onset of senescence.

Some genic effects might influence only fertility or some other strictly reproductive function having nothing to do with somatic survival. This would alter the value of the reproductive probability only for the duration of the effect, because it would not influence the probability of survival to subsequent ages. For such an effect the value of p would be determined by the duration of the effect and by the average reproductive probability per unit time in the affected period.

One of Comfort's main criticisms of Weismann's theory is that it assumed initially what it purported to explain, a declining vigor with increasing age. This is not true of the present theory, since no senescence is assumed to be initially present in the population. Each new gene, however, is judged on the basis of the current reproductive probability distribution. Any previously established genes that cause senescence will increase the rate of decline in p and make it easier for other such genes to become established. In this way senescence becomes a self-aggravating process. It must be emphasized, however, that senescence is an unfavorable character. The direct action of selection will always be opposed to it. The establishment of an important "senescence gene" in a population would cause the favorable selection of other genes that would reduce or delay the unfavorable effects. As a hypothetical example we might imagine a mutation arising that has a favorable effect on the calcification of bone in the developmental period but which expresses itself in a subsequent somatic environment in the calcification of the connective tissue of arteries. If the gene becomes established in the population and if this later effect is eventually deleterious, a selective premium would be placed on any gene that might suppress this arterial calcification. As the suppression approached completion, however, the selection pressure for further suppression would diminish. Complete suppression would probably never be realized. Senescence might be regarded as a group of adaptively unfavorable morphogenetic changes that were brought in as side effects of otherwise favorable genes, and which have only been partly expurgated by further selection. There are therefore, two opposing selective forces with respect to the evolution of senescence. One is an indirect selective force that acts to increase the rate of senescence by favoring vigor in youth at the price of vigor later on. The other is the direct selection that acts to reduce or postpone the "price" and thereby decrease the rate of senescence. The rate of senescence shown by any species would depend on the balance between these opposing forces.

The theory advanced here covers the senescence of genetically defined individuals only. It does not refer to the decline of renewable parts, such as leaves and erythrocytes, but some mention of the senescence of parts seems appropriate. It might be supposed that permanence of functional efficiency is a desirable characteristic of any part of an organism, but that it is not the only consideration. Given the necessary selective forces, it might be possible to evolve a potentially immortal erythrocyte, but some compromises would be necessary. A gene that favored erythrocyte longevity might be far from ideal for the maximization of oxygen-carrying capacity, to say nothing of unrelated functions of other systems that the gene might affect. The selective advantage of an erythrocyte that could last forever over one that could last "a very long time" might be so slight that genes favoring erythrocyte senescence might creep in because of other advantageous effects they might produce. Thus the senescence of renewable parts can also be

attributed to the natural selection of pleiotropic genes.

Testable Deductions from the Theory

The remainder of this paper will be devoted to a consideration of some expectations that follow from the theory, most of which can be tested in a preliminary way by reference to information contained in the literature. I believe that this information, although nowhere conclusive, is quite favorable to the theory.

The first four deductions relate to the phylogeny of senescence. Especially important is the implication that phylogenetic variation in senescence should be predictable on the basis of phylogenetic variation in the reproductive probability distribution. The next four relate to the physiological expectations that follow from the theory, and the last concerns the expected outcome of artificial selection for increased longevity.

(1) *Senescence should be found wherever the conditions specified in the theory are met, and should not be found where these conditions are absent.* There are organisms in which the distinction between soma and germ-plasm may not exist, but the other assumptions of the theory would seem to be inevitable for any organism, at least for any that has a clear distinction between soma and germplasm. The theory regards senescence as an evolved characteristic of the soma. We should find it wherever a soma has been evolved, but not elsewhere.

There should, therefore, be no senescence of protozoan clones. Some clones die out after a limited time, but there is reason to believe that clonal deterioration is fundamentally different from metazoan senescence. There are some strains that can apparently be propagated asexually for an indefinite period and others that cannot. Within a single species both conditions have been reported, and even among the individuals arising from a single pair of exconjugant ciliates, some will die after a few divisions and others can be propagated asexually for as long as favorable environmental conditions are maintained. No such intraspecific variation is known among metazoans. The difference between temporary and permanent clones of protozoans may apparently be due to a very few genetic factors. These various aspects of protozoan "senescence" have been reviewed by Comfort (1956: ch. 3) who concludes (p. 119)

> It is in any case probably misleading to identify the decline of protozoan cultures with the metazoan senescence which it superficially resembles. . . . There is no special reason, upon the present evidence, why the "senescence" of *Paramecium* should continue to figure as extensively as it has done in treatises devoted to gerontology.

While asexual clones should not show senescence, asexually reproducing individuals may be regarded as having somas and they should, according to the theory, show senescence. Fissile animals would appear at first sight to lack a soma, but often the products of fission are not altogether similar. It may be physiologically justified to regard one as parent and the other as offspring. The asexual reproduction of turbellarian flatworms, for example, is often termed fission, but the division is transverse and separates a head end from a quite different tail end. In some, moreover, the two parts are very unequal in size. Sonneborn (1930) interprets the division of the flatworm *Stenostomum incaudatum* as budding. Each worm gives off a small and largely undifferentiated posterior bud and retains most of the specialized tissues. The series of anterior products of division can therefore be regarded as an individual soma giving off buds. Conditions specified in the theory are met, and eventual senescence is expected of the anterior series. This appears, in fact, to be true. Sonneborn was able to keep most of the clones composed of successive posterior ends continuing for long periods of time, and none gave clear indications of death from endogenous causes. Lines of suc-

cessive anteriors, however, all died out after a limited number of posteriors had been given off.

There is a problem as to just what constitutes "the individual" in an asexual clone. From a physiological standpoint, each functionally independent system is an individual, but to natural selection, all such systems of the same genotype collectively comprise a single individual, no matter how numerous and scattered they might be. So it might be best to regard a flatworm clone as an individual and anterior series as its expendible parts.

An analogous problem exists with respect to the soma of higher plants. It is physiologically reasonable to think of a single tree as a separate individual and its demise as the death of a mortal soma. Many of the cells of a tree, however, may give rise to shoots bearing sexual cells or to structures passed on in asexual reproduction. Such potential germ cells are scattered throughout a plant. It may be that the great majority of the living cells of a plant are potential parts of the germline, because even rather specialized cell types can dedifferentiate and give rise to reproductive structures (Buvat, 1944). From the standpoint of selection and the theory developed in this paper, it would be better to regard a clone of higher plants as an individual and the separate cellulose edifices as its expendible parts. This theory demands that there be no senescence of the clone (genetically defined individual) although there should be senescence of its expendible parts (physiologically defined individuals). There is no doubt that physiologically defined individual plants undergo senescence, but the senescence of plant clones is a matter of some controversy. When Molisch wrote his classic review of plant senescence in 1928 (Molisch and Fulling, 1938), he expressed the conviction, with some reservations, that plant clones eventually deteriorate and cannot be maintained indefinitely. When the subject was reviewed again by Crocker (1942), it was indicated that many of Molisch's examples of clonal senescence had been attributed to exogenous causes. Some clones, for instance, deteriorated because of virus diseases that were passed on in asexual reproduction but not through seeds. In regions that were free of these diseases, the clones continued to thrive.

It will probably be a long time before this matter is completely settled. Nevertheless, it can be concluded that if a plant clone undergoes senescence at all, it must be very slow compared with the senescence of the separate individuals of the clone. As Crocker pointed out, many horticultural varieties, which live as isolated plants for only a few years or decades, have been propagated asexually for centuries and are still vigorous.

(2) *Low adult death rates should be associated with low rates of senescence, and high adult death rates with high rates of senescence.* Cumulative adult mortality is the primary reason for decline in reproductive probability with the passage of time. If, as I have indicated, the rate of this decline determines the balance of selective forces acting on senescence at any given age, we should be able to predict rates of senescence on the basis of adult mortality rates.

This expectation is obviously realized, if it is legitimate to compare widely different kinds of organisms. Active adult insects have mortality rates of the order of ten percent per day (Lack, 1954: 102), and maximum longevity is of the order of a few weeks (Comfort, 1954: 57). Mortality rates of adult man in extremely primitive situations probably never averaged more than ten percent per year, and man's maximum longevity may include as many years as that of the insects includes days. In wild populations generally, it probably seldom happens that senesence has more than a slight modifying influence on mortality. The death rates of young adults are usually such that very few individuals will live long enough to suffer any gross debilitation through the process of senescence (Lack, 1954).

The critical comparison would be be-

tween organisms that have approximately similar life cycles except for adult mortality rates. Birds have lower adult mortality rates than mammals of similar size (Lack, 1954; Blair, 1948; 1951), and, as expected, greater potential longevity (Comfort, 1956: 160). The difference in senescence rate has been attributed to some fundamental difference between the physiological organizations of birds and mammals, perhaps to differences in the manner of growth limitation (Comfort, 1956: 160). For reasons discussed below, however, I believe it is unlikely that any single physiological difference is responsible. The evolutionary cause of the low rate of bird senescence must be that birds can fly, are thereby less liable to predation and accidents, and therefore have lower mortality rates. Decisive evidence would come from a detailed investigation of the rates of senescence of flightless birds, for which high rates of senescence would be expected, and flying mammals, for which low rates would be expected. No such investigation has been carried out, but the evidence, although meagre, is extremely suggestive. Of 45 non-passerine birds for which Comfort (1956: 50) lists reliable age maxima, only two, the ostrich and the emu, are flightless, and these are among the four with the lowest age maxima. Large animals are usually longer-lived than small ones, and on this basis the ostrich and emu should live longer than any of the other birds in Comfort's list. If such age maxima are a reliable basis for comparison of senescence rates, a causal relationship between flightlessness and rapid senescence is clearly indicated.

The most volant mammals are the bats. There are no reliable records of bat age maxima, nor studies of mortality rates in the wild. Ringed bats, however, have been recovered after as long as seven years (Lack, 1954: 100), a period that exceeds the age maxima of other small mammals such as rodents and insectivores (Comfort, 1956: 47). Bats must be significantly longer-lived than other mammals of comparable size and developmental rates.

Other special life-history features can affect mortality rates, and such features should therefore influence the evolution of senescence. The shells of turtles presumably reduce their vulnerability to predation and fatal injury. This may account for their great longevity compared with other reptiles, even with very large ones like crocodilians. Relatively small tortoises have a maximum life-span of twice that of the alligator (Comfort, 1956: 51–2). Such factors as homing and territoriality could also affect adult mortality rates and the balance of selective forces acting on senescence. If an animal has occupied an individual niche for a long time it is likely, by virtue of the long-continued survival of the animal, that the niche is an especially favorable one. The probability that it will continue to be favorable for one more year increases with each passing year. Such factors as these would act to lower mortality rates for the higher age groups and intensify the selection against senescence. Such a declining adult mortality rate has been demonstrated for territorial lizards (Stebbins, 1948).

According to the theory, death rates prior to maturation have no influence on the evolution of senescence. The larger fishes and the very prolific marine invertebrates have enormously high mortality rates in the young stages, yet such organisms may live for a long time in captivity (Comfort, 1956: ch. 2).

(3) *Senescence should be more rapid in those organisms that do not increase markedly in fecundity after maturity than those that do show such an increase.* Many organisms, such as rotifers, most insects, and warm-blooded vertebrates grow very little after reaching maturity. Others, such as mollusks, most crustacea, and most cold-blooded vertebrates continue to grow at an appreciable rate long after sexual maturity, perhaps throughout life. Such an increase in size is accompanied by an increase in fecundity. An

old carp may produce ten times as many eggs as a recently matured one (Carlander, 1953). An increase in fecundity has the opposite effect from mortality. It tends to increase the reproductive probability for the more advanced ages and thereby intensify the selection against senescence. This, I believe, is the basic evolutionary reason for the apparent association between rapid senescence and determinate growth (Comfort, 1956: ch. 5).

(4) *Where there is a sex difference, the sex with the higher mortality rate and lesser rate of increase in fecundity should undergo the more rapid senescence.* Males of many animals are exposed to greater risks than females. They may fight each other or spend much time in conspicuous courtship displays, and they may be more conspicuously colored than the females. All these factors would increase the dangers from predation, and any actual combat, of course, may be dangerous in itself. A greater adult mortality rate of males is known for a number of wild populations of species to which these considerations apply (Haskins and Haskins, 1951; Krumholz, 1948; Lack, 1954: 111–12) although female mortality rates seem to be higher in birds (Lack, 1954: 107–11). Likewise, the number of offspring produced by a male is presumably less dependant upon body size than it is in the female, at least where there is internal fertilization. All these factors would make the rate of decline in reproductive probability more rapid in males than in females. The balance of selective forces should therefore result in more rapid senescence in the males of species in which these conditions are found, and in which the genetic and hormonal mechanisms provide for sex differences in such characters.

Throughout the animal kingdom it is a general rule that females are longer-lived than males; so it would appear that the theoretical expectations are realized. There are some possible exceptions, and unfortunately both the rule and exceptions are based on scanty data (Comfort, 1956: 30–4). It is certain, however, that the females of really well studied animals, such as man, farm animals, and the fruit-fly are longer-lived than the males. The theory of senescence as a function of the reproductive probability distribution may explain sex-differences in vigor in old age, but it does not explain the frequently observed differences in vigor early in life, such as the greater fetal and infant mortality of human males.

(5) *Senescence should always be a generalized deterioration, and never due largely to changes in a single system.* The earlier an adverse genic effect, the greater will be the associated p-value and the intensity of adverse selection. So if the adverse genic effects appeared earlier in one system than any other, they would be removed by selection from that system more readily than from any other. In other words, natural selection will always be in greatest opposition to the decline of the most senescence-prone system. If, for instance, degenerative changes in the endocrine glands were the primary cause of human senescence, there would be little selection against the deterioration of other organs. The selective forces against senescence would be directed primarily against that of the endocrine system. This selection and the accumulation of harmful genetic effects in other systems would cause the senescence rate of the other systems to approach that of the endocrine glands.

Formerly it was believed that mammalian senescence was largely a hormonal phenomenon. Miraculous rejuvenation was anticipated from the implantation of young gonads into aged people, but the miracles were never realized. It was also thought by some that a deterioration of the nervous system was the primary cause of senescence in certain insects. Comfort has shown, however, that there is little evidence for these beliefs. For insects he lists (1956: 96–7) several known types of senile deterioration, including "general senile decay." In mammals and especially man it is now realized that senescence

characterizes many organs and systems, perhaps all (Comfort, 1956: ch. 6; Lansing, 1952: ch. 8–30). More evidence is needed for other organisms, however.

Comfort (1956: 98) points out that death in insects that do not feed during the imaginal stage must eventually result from a depletion of food reserves. This is true, but according to my theory there should be other degenerative changes in addition to the food depletion. It would be expected that death in natural populations would result from these other changes about as often as from the food depletion. Otherwise there would be intense selection favoring greater food reserves. It would also be predicted that artificial replenishment of food reserves would not lengthen life to any significant degree.

Basic research in gerontology has proceded with the assumption that the aging process will be ultimately explicated through the discovery of one or a few physiological processes. Medawar (1955) clearly expressed this basic assumption. He envisioned the essential task of gerontologists to be that of distinguishing cause from effect among the multitude of observable changes in aging organisms, and eventually isolating the presumably few ultimate causes. Any such small number of primary physiological factors is a logical impossibility if the assumptions made in the present study are valid. This conclusion banishes the "fountain of youth" to the limbo of scientific impossibilities where other human aspirations, like the perpetual motion machine and Laplace's "superman" have already been placed by other theoretical considerations. Such conclusions are always disappointing, but they have the desirable consequence of channeling research in directions that are likely to be fruitful.

(6) *There should be little or no post-reproductive period in the normal life-cycle of any species.* This prediction is a special case of the one immediately preceding, since sterility is the selective equivalent of death. If most of the senescence-influenced removal of individuals from the breeding population were due to a deterioration of the reproductive system, there would be a greater selection against this deterioration than any other. The population would evolve towards increased reproductive and decreased somatic longevity.

At first sight it appears that this prediction is not realized. Long post-reproductive periods are known in many domesticated animals and in man himself. In man it may even be longer than the reproductive period. However, these observations lose much of their seeming importance when it is realized that they are largely artifacts of civilization. In very primitive conditions, such as prevailed throughout almost all of man's evolution, post-reproductive individuals were extremely rare. Of 173 paleolithic and mesolithic skeletal specimens whose age at death could be determined, Valois (1937) found only three who were over fifty, and none was much older than this. It is safe to conclude that senile sterility became an important factor in removing individuals from the human breeding population only in recent historical times.

The term *post-reproductive* needs clarification with respect to man. There is more to reproduction than producing viable gametes. In man there is a very long period of dependance after conception. Any individual, of whatever age, who is caring for dependent offspring is acting in a way that promotes the survival of his own genes and is properly considered a part of the breeding population. No one is post-reproductive until his youngest child is self-sufficient. So the post-reproductive period in man begins not with senile sterility, but at least a decade later.

In the human male and in both sexes of other animals, reproductive decline is a gradual process (Comfort, 1956: 177–8), as is the senescence of other systems. In the human female, however, it is rather abrupt, and some special explanation is required. At some time during human evolution it may have become advantage-

ous for a woman of forty-five or fifty to stop dividing her declining faculties between the care of extant offspring and the production of new ones. A termination of increasingly hazardous pregnancies would enable her to devote her whole remaining energy to the care of her living children, and would remove childbirth mortality as a possible cause for failure to raise these children. Menopause, although apparently a cessation of reproduction, may have arisen as a reproductive adaptation to a life-cycle already characterized by senescence, unusual hazards in pregnancy and childbirth, and a long period of juvenile dependence. If so, it is improper to regard menopause as a part of the aging syndrome.

The long post-reproductive periods of domesticated animals are also the products of civilization. The rat has a long post-reproductive period in a man-made environment where blindness, extensive paralysis, and other gross functional impairments do not result in death, but this is clearly not of the same significance as such a post-reproductive period in a wild individual.

A related problem is that of castration. Castration, of course, immediately reduces the reproductive probability to zero, but it is only through selection that such an effect could hasten senescence. If castration were persistently performed at a certain age, it would remove all selection against senescence following that age. After a large number of generations an increased rate of senescence would be expected after the age of castration.

Such an experiment has been performed by nature in the development of uniparous animals and monocarpic plants. For every individual of such species, the immediate reason for reproducing only once is that once it reproduces it dies. Historically, however, it must have been the other way around. The lack of a second period of reproduction in the normal life-cycle removed all selection against senescence following the first reproduction. Eventually this resulted in a uniparous or moncarpic life-cycle through an extremely rapid senescence following the first period of reproduction. Such conditions probably arise gradually. Heavy mortality between the first and second breeding seasons lowers the reproductive probability for the second season relative to the first. This in turn favors the development of senescence between the two breeding seasons, and this further lowers the probability of a successful second reproduction. Eventually the complete loss of the second period of reproduction might not be a serious disadvantage, and might be brought in as a pleiotropic effect of a gene that conferred some slight advantage during the first season. A possible transitional condition is shown by the Pacific steelhead trout, which spawns in the same streams as the salmon *Oncorhynchus kisutch*. The trout, unlike the salmon, does not die right after the first spawning. It may return to the sea and undertake a second spawning migration the following year. The chances of a repeat spawning are low, however. The first spawners were five times as numerous as all other age groups combined in a spawning steelhead population studied by Shapovalov and Taft (1954).

(7) *The time of reproductive maturation should mark the onset of senescence.* Senescence is regarded in this paper as a consequence of the decline of reproductive probability with increasing age. This decline starts at the time of reproductive maturation. So senescence should also begin at this time.

This expectation would be very difficult to test at present, since no precise measurement of senescence has been developed. The life-table demonstration of increasing probability of death with increasing age is subject to some serious criticisms but remains the best available measure of senescence (Medawar, 1955). It is reliable only when different age classes are exposed to the same kinds and degrees of dangers and stresses. Since such factors are seldom completely controlled, the life-table can be relied on only for studying very marked functional impairments with the passage of time.

Moreover, senescence is not the only factor responsible for variations in vigor at different ages. All through development there must be compromises between the need for continuous fitness and the demands of morphogenesis. The modern human mortality rate is extremely high in infancy, a period of rapid morphogenesis. It then declines to a minimum at ages ten to twelve, rises during adolescence, and continues to rise with increasing rapidity thereafter (Comfort, 1956: 16). This distribution of death rates might be taken as verification of the theory, but adolescence is a period of more rapid morphogenesis than that immediately preceding, and this factor may be partly responsible for the increased adolescent mortality. Moreover, the distribution of stresses and dangers is hardly uniform through childhood, adolescence, and early adulthood.

In many primitive human societies the death of teen-age parents must have greatly reduced the survival prospects of any children they might have produced. The care of dependent offspring is as important to human reproduction as the production of gametes. So the rate of decline in reproductive probability in early adulthood must be very slight, and this factor should result in a very low rate of senescence during the first decade of man's reproductive life.

Comfort (1956: 39–40) maintains that any theory of senescence based on natural selection demands that the age of minimum mortality and that of maximum fertility should coincide. He casts doubt on such theories because human life-tables fail to confirm this expectation. This argument is surely fallacious. Vigor at age ten is no less important to human reproduction than vigor at age twenty-five. In fact it is more important. Vigor at ten affects the value of the entire reproductive probability. Vigor at twenty-five affects only the part of reproductive probability that follows that age.

(8) *Rapid individual development should be correlated with rapid senescence.* Reproductive maturation is the most important landmark in the life-cycle for the evolution of senescence. Senescence may theoretically begin right after this stage in development. So the sooner this point is reached, the sooner senescence should begin, and the sooner it should have demonstrable effects. This is, perhaps, another reason for the apparently slow senescence of birds. They grow very rapidly to maximum size, but sexual maturity does not occur until long after this maximum size is reached.

Senescence has long been considered an aspect of morphogenesis (see Comfort, 1956: 7–8, for references), although the precise meaning of this relationship has never been clarified. In this paper I have assumed that genes produce different effects in different somatic environments, and that these effects become progressively less controlled by selection with increasing adult age. If senescence is actually due to the morphogenetic effects of genes, conditions that favor rapid morphogenesis should also favor rapid senescence, not only by reducing the time required to reach maturity, but during the adult stage as well. The rate of recognizable morphogenetic change in the adult, such as the obliteration of bone sutures in man, should therefore correspond to the rate of senescence.

The idea that the rate of senescence depends in some way on the "rate of living" has been recognized for many years. It appears that there is some sort of fixed quantity of vital vigor that can be expended at different rates. Comfort (1956: ch. 5) advanced three hypotheses as to the nature of this life quantity: (1) an unrenewable store of some vital necessity (2) a metabolic quantity, measurable, perhaps, in calories (3) a fixed developmental sequence. Since the first suggestion was not made specific enough to discuss very critically, the choice is mainly between the remaining two. According to my theory, the third alternative is the correct one. It would be expected that if development could be completely arrested, there would be no senescence, and that if development were greatly accelerated,

without a commensurate increase in metabolism, senescence would be accelerated and appear at the usual developmental stage.

Senescence of monocarpic plants can be greatly delayed by preventing them from forming flowers and seeds (Crocker, 1942). The eel may live 55 years in captivity (Comfort, 1956: 53), where conditions necessary for spawning are not found, but wild ones usually spawn and die at about ten years, and never more than twice this age (Frost, 1950). An eel kept for half a century at room temperature surely performs an enormously greater feat of metabolism than a wild one in ten years. If the immediate post-reproductive death of organisms that reproduce only once is considered senescence, and if the pre- and post-reproductive periods are considered morphogenetic stages, these observations on eels and monocarpic plants indicate a causal relation between delayed morphogenesis and delayed senescence.

A direct relationship between rates of morphogenesis and of senescence is also indicated by Lansing's (1947) evidence of a cytoplasmically inherited factor that influences both longevity and rate of development of rotifers.

(9) *Successful selection for increased longevity should result in decreased vigor in youth.* If senescence results from genes that increase youthful vigor at the price of vigor later on, the loss of some of these genes through selection should result in decreased youthful vigor. It does not follow that puny youths are necessarily long-lived, nor that very old individuals were necessarily below average in youthful vigor. Most of the genes or gene combinations that favor vigor early in life probably also favor longevity. Only a small proportion of the genes need be of the sort that produce opposite effects on fitness at different ages, and of these, only a certain proportion would have available alleles that could reduce the rate of senescence. It follows that an individual can not be exceptionally gifted with both youthful vigor and long life. I would predict that no human being who is over a hundred years old was unusually vigorous as a young adult.

Summary

A new individual entering a population may be said to have a *reproductive probability distribution.* The reproductive probability is zero from zygote to reproductive maturity. Later, perhaps shortly after maturity, it reaches a peak value. Then it declines due to the cumulative probability of death. There is a cumulative probability of death with or without senescence.

The selective value of a gene depends on how it affects the total reproductive probability. Selection of a gene that confers an advantage at one age and a disadvantage at another will depend not only on the magnitudes of the effects themselves, but also on the times of the effects. An advantage during the period of maximum reproductive probability would increase the total reproductive probability more than a proportionately similar disadvantage later on would decrease it. So natural selection will frequently maximize vigor in youth at the expense of vigor later on and thereby produce a declining vigor (senescence) during adult life. Selection, of course, will act to minimize the rate of this decline whenever possible. The rate of senescence shown by any species will reflect the balance between this direct, adverse selection of senescence as an unfavorable character, and the indirect, favorable selection through the age-related bias in the selection of pleiotropic genes.

Variations in the amount of fecundity increase after maturity, in the adult mortality rate, and in other life-history features would affect the shape of the reproductive probability distribution and thereby influence the evolution of senescence. Any factor that decreases the rate of decline in reproductive probability intensifies selection against senescence. Any factor that increases the rate of this decline causes a relaxed selection against

senescence and a greater advantage in increasing youthful vigor at the price of vigor later on. These considerations explain much of what is known of phylogenetic variation in rates of senescence.

Other deductions from the theory are also supported by limited available evidence. These include the expectation that rapid morphogenesis should be associated with rapid senescence, that senescence should always be a generalized deterioration of many organs and systems, and that post-reproductive periods be short and infrequent in any wild population.

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A CASE OF DARWINIAN SELECTION IN BEARS

BJÖRN KURTÉN

Geological Institute of Helsingfors University, Finland

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INTRODUCTION

Differential survival or mortality is one aspect of selection, not the only one but of great importance. It is the same concept as Darwin's and Wallace's "survival of the fittest" and may properly be styled Darwinian selection. Such differential survival may favor variants close to the population mode, while weeding out more extreme variants through higher mortality rates than the population average. This is "stabilizing" selection, as it is sometimes called; centripetal selection (Simpson, 1954) would seem to be a happier expression. A population in this situation is, on an average, well-adapted; the selection tends only to promote the central or most frequent type in the population. As another possibility, a linear component (*ibid.*) may enter into the complex. The selection is then directed towards an optimum different from the population mode, within or outside the realized population range of variation. Such instances are apparently less common, because a population of this type is not optimally adapted, and will tend to adapt by utilization of its genetic variability; if no suitable variability is available, it is rather likely to become extinct.

Instances of differential survival affecting mammalian teeth have been given in Kurtén (1953, 1955 b). The study of differential mortality is particularly easy on mammalian tooth crowns, because variation caused by growth does not occur. If care is taken to select a mensuration system not affected by the wear or by the disposition of the tooth in the jaw, any significant reduction of variation or change of mean in a cohort, with increasing age, is therefore due to differential survival, or Darwinian selection.

A necessary prerequisite for study of this kind is the existence of large and homogeneous samples, because the changes in variances and means are generally subtle, and only a large material can be used for the statistical establishing of such trends. It should also be possible to make some kind of age grouping, even if only a crude distinction between "young" and "old" individuals, with unworn and worn tooth crowns, respectively.

MATERIAL AND METHOD

The European cave bear (*Ursus spelaeus*) is exceptionally useful in quantitative population studies. Very large accumulations of fossils are known, and each cave sample represents a local deme and a geologically very short time span, probably on the order of 5,000–30,000 years for most caves; thus a high degree of homogeneity is ensured. The great accumulations of fossils result from very intensive sampling out of a continuously rather small population (Soergel, 1940). Most caves were only inhabited during hibernation, and a study of the age distribution (which will be published in detail elsewhere) indicates that there was a mortality peak near the end of the hibernation period; the fossils show an age grouping with modes at roughly 0.4, 1.4, 2.4 etc. years of age.

Thus we have not only statistically respectable samples, but also the means to make reasonably secure determinations of individual age, and thus study the trends of Darwinian selection during annual intervals in the life history of the cohort.

In my previous studies of Darwinian selection in bears, absolute dimensions of teeth were used. It was then necessary to

use sexually homogeneous samples, in order to avoid the effects produced by sex dimorphism. The study is thereby limited to sexable material, and this approach is not practicable for many cave bear samples, which consist mainly of isolated teeth —particularly the youngest individuals. Isolated teeth cannot be sexed, except canines and some incisors. Other methods must be devised for a study of differential mortality on such samples.

Regression analysis was found to be useful and highly illuminating. For the present purpose, however, the less laborious and more easily understood quotient method will be used. This reduces the possibilities for study, insofar as only dimensions with an isometric or nearly isometric interrelationship can be used. The characters which will be discussed here belong to this group. The method is to express one of the dimensions in per cent of the other, and study the changes in the variation and average value of this index with increasing age in the cohort. The initial stage (cohort at about 0.4 year) is represented by the complete sample, and the succeeding annual groups are obtained by successively subtracting from the sample the 0.4-year group, 1.4-year group, and so on.

The sample used in this study was excavated long ago in the caves near Odessa (Nordmann, 1858–60; Kurtén, 1955 a, b), and the material is in the Nordmann Collection of the Geological Institute of Helsingfors University. The study of this material has been sponsored by grants from the Academy of Finland and the Finnish State Commission of Natural Science.

Evidence of Selection in the Second Molars

The index of 100× length of M^2 paracone/total length of M^2 crown, which will be called the paracone index, was computed for the Odessa material. The paracone, or anterior external cusp, is the largest cusp of the posterior upper molar (fig. 1). The index expresses its length as a percentage of the total crown length. The dimensions could be adequately and consistently measured on most of the material except a few specimens in stages of excessive attrition, which were left out of consideration.

Fig. 1. Left second upper and lower molars of cave bear, *Ursus spelaeus*, external view. The paracone (pa) of the upper molar occludes into the valley between protoconid (prd) and hypoconid (hyd) of the lower.

The change in the mean and standard deviation for this index with increasing age in the cohort is shown in table 1. The standard deviation (σ', see Simpson and Roe, 1939) shows a slow but steady reduction of variation throughout the series, not of high statistical significance but nevertheless, as a trend, highly suggestive. That Darwinian selection did occur is however conclusively proved by the fact that the mean also changes in the cohort, and this change is highly significant. The mean for the group that died at 0.4 year is 29.26 ± 0.20, and differs from, for instance, the cohort mean at 2.4 years (see the table) with the highest significance ($P < 0.001$). There is a continuous reduction in the mean paracone index with

Table 1. *Paracone index for the Odessan* Ursus spelaeus *cohort, at successive ages*

Age (years)	N[a]	M	σ
0.4	109	28.87 ± 0.16	1.70 ± 0.11
1.4	43	28.27 ± 0.26	1.69 ± 0.18
2.4	27	27.50 ± 0.27	1.39 ± 0.19
4.4	18	27.33 ± 0.31	1.30 ± 0.22
6.4	10	27.30 ± 0.36	1.14 ± 0.25

[a] N, number of specimens; M, mean; σ, standard deviation.

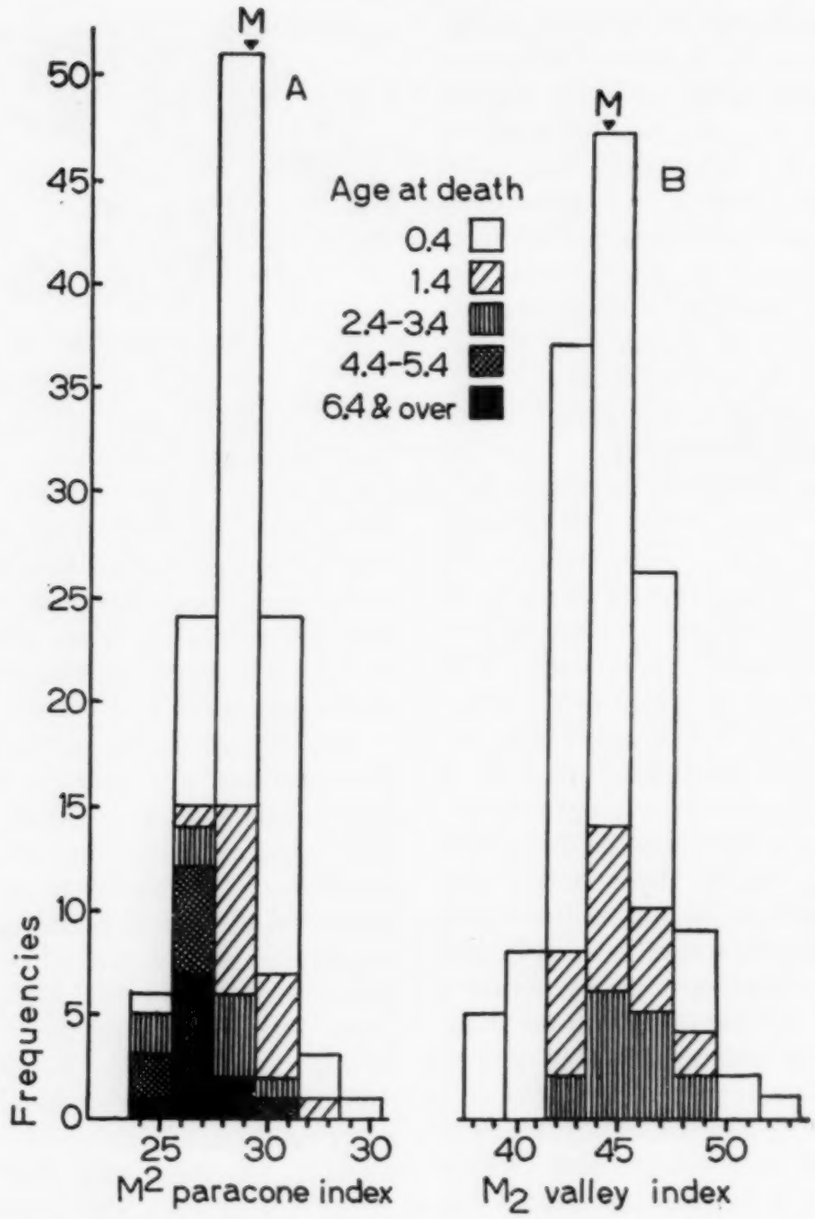

FIG. 2. Differential survival affecting the paracone and valley indices for M^2 and M_2 respectively (A and B). The diagrams represent the variation found in the cohort at successive intervals, as labelled. M, mean for total sample.

increasing age, particularly strong during the first interval, but continuing up to the last stage recorded. The trend is depicted graphically in the distribution diagram, fig. 2 A.

The result can hardly be spurious as a result of wear, because the greatest change occurs during the initial stages, in which even the summit of the paracone is hardly touched by wear at all, and still less the notches demarcating the base of the cusp, where the measurements were taken. This means that there was strong linear selection in favor of a lower paracone index, and hence a relatively smaller paracone, than the population average. Practically all the individuals with a paracone larger than the initial cohort mean died before 6–7 years of age, whereas the rate of survival is much higher in the group with less than medium-sized paracones (fig. 2 A).

What is the cause of this intense selection, and why does it begin so early in life?

The interval 0.4–1.4 years is the time when M^2 emerges. At its beginning, only the fore part of the tooth protrudes. However, the paracone is the first part of the tooth to emerge, and it is already in functional occlusion at this time. Thus, if a large paracone was actually inadaptive, selection might well begin at this early date, and continue until most of the inadaptive individuals have died.

The cause of the selection may be sought in the interaction of M^2 and M_2; the latter occludes with the anterior part of the former, as shown in fig. 1. The paracone of M^2 bites between the protoconid and hypoconid of M_2, and is received by the notch or valley between these cusps. Obviously the paracone should fit well into this receptacle, if the occlusion is perfect.

This suggests at once that the paracone may have been, on an average, slightly too large to fit easily into the valley in M_2. As a corollary, the size of this valley should also be affected by selection, the trend here being the converse.

This was tested by an analogous method. The distance between the summits of protoconid and hypoconid of M_2 was measured, and the index $100\times$ this distance/total crown length of M_2 was computed (the M_2 valley index).

The M_2 valley index could be obtained for the three initial age groups only, because the tips of the cusps become obliterated by wear in older groups, and the length of the valley becomes indeterminate. The trend for the series 0.4–2.4 years is however definite (table 2). There is a marked change in the mean value of the index, and the difference between the individuals that died at 0.4 year (mean $= 43.90 \pm 0.26$) and the survivors at 1.4 and 2.4 years is significant ($P \leqslant 0.01$). There is also a reduction in the variation, suggesting centripetal selection; but the shift of the mean, and the asymmetry of the survival (fig. 2 B) reveal a strong linear component in selection.

TABLE 2. *M_2 valley index for the Odessan* Ursus spelaeus *cohort, at successive ages*

Age (years)	N	M	σ
0.4	137	44.19 ± 0.22	2.55 ± 0.15
1.4	36	45.00 ± 0.34	2.06 ± 0.24
2.4	15	45.53 ± 0.52	2.03 ± 0.37

TABLE 3. *Comparison of survival for individuals with paracone and M_2 valley indices below and above population mean. As a standard, an estimate of the actual survival in the population is given, based on all available material*

	Survival in per cent				
	Paracone index		M_2 valley index		
Age in years	<M	>M	<M	>M	Survival estimate[a]
0.4	100	100	100	100	100
1.4	48	29	17	38	61.8
2.4	39	6	4	20	47.8
4.4	26	4			31.1
6.4	16	2			23.0

[a] This estimate shows higher survival figures, because accurate measurements could not be taken on some of the worn teeth. The discrepancy is particularly great for M_2, of which no specimens older than 2.4 years could be measured.

DISCUSSION

We may now, as it seems, conclude that the average condition in the population was one of slight malocclusion between paracone in M^2 and corresponding valley in M_2, the latter being slightly too small for the perfect reception of the former. Individuals with a relatively small paracone and/or a relatively large M_2 valley had undisturbed occlusion, and survived. As a result, selection acted simultaneously on both teeth, favoring on one hand second upper molars with relatively small paracones, on the other hand second lower molars with a relatively wide notch between the external cusps.

In view of the seeming triviality of these characters, the great strength of this selection, and the early age at which it began, appear rather astonishing. Darwinian selection began immediately when the teeth entered into function, and weeded

out most inadaptive variants in a few years. The longevity of a cave bear tooth cusps was not great; in a few years it wore down and the occluding surfaces were moulded against each other. The work of selection, however, was finished before that; the great harvest of mass mortality in early life was intensely selective, and acted precisely on the cusp pattern of the teeth. Note also that the effect of this kind of selection on reproduction and hence evolution must be intense, provided that suitable genetic variation is at hand, because the main part of the differential mortality occurred before sexual maturity (3–4 years). Table 3 indicates, for instance, that the survival to sexual maturity for individuals with paracone index lower than the population mean was more than six times higher than the survival of those with an index above the mean. A great majority of the individuals in the breeding population would therefore have consisted of individuals with relatively small paracones in M^2. This gives an insight into the causes of the evolutionary plasticity and intraspecific stability of mammalian dental patterns, qualities which obviously arise from potent and subtle selective control.

What, then, was the effect of Darwinian selection in the present instance? The remains from Odessa represent hundreds, probably thousands of individuals. The period of deposition must have been on the order of many thousand years. If suitable genetic variation existed in this population, it seems that the intense selection would inevitably have taken rapid effect. A shift to a new genotype, producing harmoniously occluding teeth as a population average, would have been expected in a few generations. It is clear that this did not happen, for then most of the teeth would have been sampled from a well-adapted population, and the skewed survival of the earliest generations would have been quite over-shadowed by normal survival in hundreds of later generations.

It seems most likely that suitable genetic variation was not available in this population, and it is thus probable that these characters were not controlled by polygenes. Similarly, a series of allometry studies (Kurtén, 1954 a, b, 1955 a, and unpublished) suggest that intradental allometries are not always and perhaps not even usually governed by polygenes.

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WHAT, IF ANYTHING, IS A RABBIT?

ALBERT E. WOOD [1]

Biology Department, Amherst College, Amherst, Mass.

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INTRODUCTION

The title of this paper is slightly modified from that of an article I encountered some years ago, which appeared to be approaching the problem of the relationships of the Lagomorpha, or rabbits and their relatives, from the most basic point of view. This paper, entitled "Gibt es Leporiden?", seemed to be questioning the very existence of such animals. Investigation showed, however, that the question involved was not whether members of the family Leporidae existed, but whether rabbit-hare hybrids did (E.B.C., 1908). Since then, I have met no one who questions the existence of rabbits and hares, and I have been reluctantly forced to accept them. Furthermore, there seems to be no question but that they are mammals. But just where, among the mammals, they belong is still unsettled.

Unfortunately, there is no good popular name for the order, "rabbit" being also used for those genera of leporids that are not hares. Perhaps "bunny" is the best vernacular name for the lagomorphs, for which it is already used at times.

This group of animals are currently referred to an order, the Lagomorpha, containing only two living families, the Leporidae or rabbits and hares, and the Ochotonidae or pikas. The lagomorphs are a rather distinctive group, and there rarely seems to be any question as to whether any given animal is or is not a lagomorph.

Both families have been traced back to the Oligocene, and both seem to have had a basic Holarctic distribution then as well as now. At that time they were, naturally, closer to each other than they are at present, but they were still distinct, and there are only one or two genera where there have been disagreements as to familial allocation (compare Burke, 1936, p. 152 and Wood, 1940, pp. 345–348 with Bohlin, 1942, pp. 40–70).

In the upper Eocene, the genus *Mytonolagus* is known from North America, and *Shamolagus* and *Gobiolagus* from Mongolia. Here there is more question as to familial allocation, but, for present purposes, their precise allocation is immaterial. Earlier than upper Eocene, no fossil representative of either family is known.

A number of specimens are known from the upper Paleocene of Mongolia, belonging to the genus *Eurymylus*, for which Matthew, Granger and Simpson (1929, p. 5) established the family Eurymylidae. *Eurymylus* shows some leporid and some ochotonid characters, as well as a number of features of its own, such as the absence of P^2, which rule it out from ancestry to the later members of the order. Although the material is very fragmentary, there seems to be no question but that it represents a lagomorph (for a review of this question, see Wood, 1942). Unfortunately, all the known material is so broken that it cannot be determined how many upper incisors were present (i.e., the statement by Colbert, 1955, p. 301, is presumably a misprint for "second upper premolar").

Bohlin has recently (1951) described a genus, *Mimolagus*, from beds of unknown age in Kansu. This seems surely to be a eurymylid, but differs from the type genus, among other respects, in possessing P^2. The snout is preserved, and there

[1] This work was assisted by grants from the National Science Foundation and from the Marsh Fund of the National Academy of Science.

were apparently alveoli for a second pair of incisors behind the principal pair. Unfortunately, while some specimens of *Eurymylus* have little-worn lower cheek teeth, all the upper teeth of both genera are so badly worn that very little can be told of their basic tooth pattern, beyond the fact that they are not fundamentally dissimilar to the lower Oligocene forms.

Before considering the possible relationships of the Lagomorpha, it would be well to determine just what their basic characters may be. A set of diagnostic criteria might be as follows: gnawing mammals, with ever-growing incisors but weak masseter and temporal muscles, the former not readily subdivisible; jaw movements vertical or transverse, with the glenoid fossa short anteroposteriorly; dental formula I 2/1 C 0/0 P 2-3/2 M 2-3/2-3; upper tooth rows farther apart than lowers; lower teeth in plane of ascending ramus; unilateral hypsodonty of upper teeth, with very low-crowned buccal sides which become reduced out of existence early in lagomorph evolution; upper cheek teeth made up of cusps of very uncertain homologies, which have not been demonstrated to be tritubercular in origin; a third pair of incisors present, which is ephemeral, being quickly replaced by the permanent incisors; upper incisors in premaxilla only; lower incisors of variable length, ending below P_3 in leporids, below P_4 in ochotonids, and below M_2 in *Eurymylus;* microscopic structure of enamel of incisors with only one layer of enamel instead of two as in rodents; sides of maxillae on snout fenestrate—highly so in leporids, with one large fenestra in ochotonids, and with merely incipient fenestration in *Eurymylus;* elongate incisive foramina, whose rear end lies between the cheek tooth rows; short palate, extending in the midline only as far as P^4 or M^1; well developed supra-orbital processes; no entotympanic, bulla being formed from the ectotympanic alone; rami solidly united, with no possible movement at the symphysis; no epicondylar foramen on humerus; tibia and fibula fused in all cases where they are known (i.e., since the Oligocene); fibula articulates with calcaneum; caecum possessing a spiral valve; no os penis; and scrotum prepenial.

Previously Suggested Relationships of Lagomorphs

The original students of classification included the lagomorphs among the rodents. The first recognition of their separateness was by Illiger, who separated them as one of eight families of rodents, to which he gave the name Duplicidentata.[2] This group was raised to subordinal level by Waterhouse (1842). The division of the rodents into four suborders—Lagomorpha, Sciuromorpha, Myomorpha and Hystricomorpha—dates from Brandt (1855). Subsequent authors tended to divide rodents into Duplicidentata, the Lagomorpha; and Simplicidentata, the Sciuromorpha, Myomorpha and Hystricomorpha, based on the distinctions included in the list of lagomorph characters just cited, but epitomized by the presence of two upper incisors.

Tullberg, in his monumental review of the rodents, obviously was impressed by the differences between the Duplicidentata and Simplicidentata (1899, pp. 336–338), but finally decided to leave them together largely because of embryological resemblances (p. 337). He pointed out, however, that their anatomical similarities, other than that they both were gnawers, were not very striking. He noted that there are other groups of mammals, including Typotheres, *Chiromys* and *Phascolomys,* which are more rodent-like in their incisors than are the Lagomorphs. He did not feel that there were any very striking similarities between Duplicidentates and Simplicidentates in cheek tooth pattern, and that the differences in their methods of chewing are so great that they must have had distinct origins. He then concluded that the embryological similari-

[2] This paragraph is based extensively on Simpson, 1945, p. 196. References to the works here cited may be found in his bibliography.

ties between the two groups are so striking, however, that they must be closely associated, especially since neither has any other group to which it could be considered related. Finally (p. 338) he stated that the fact that, in his opinion, both Duplicidentates and Simplicidentates were descended from a common ancestor, should not be interpreted as implying that this common ancestor was a gnawer, but that the gnawing ability was developed by both groups independently. In modern terminology, Tullberg would certainly have considered the two groups to be distinct orders, independently derived from, perhaps, the insectivores.

The first formal separation of the lagomorphs from the rodents was made by Gidley (1912). This was based on the dental formula, particularly the incisors; palate; glenoid fossa; structure of the caecum; antero-posterior motion of elbow-joint; fusion of tibia and fibula; and fibular-calcaneal articulation. Gidley then suggested (p. 286) that both Lagomorpha and Rodents were very ancient orders, with no particular relationships to each other, and, further, that there are a number of similarities between the Lagomorpha and the Artiodactyla. Some of these last similarities, as Gidley indicated, had previously been commented on by Cope (1884, p. 813).

Gradually, Gidley's point of view of the ordinal independence of the Lagomorpha has been more and more widely adopted. In addition to the features cited by Gidley, there are a number of other striking differences, including the strength and differentiation of the masseter; the enamel structure of the incisors (Korvenkontio, 1934); and the peculiar pattern of the lagomorph cheek teeth. The earlier rodents actually have fewer characters in common with the lagomorphs than do the later ones, the only features that unite them being the gnawing incisors and the fact that both are otherwise fairly primitive mammals. This last item covers such features as the generally primitive nature of the brain, the presence of a uterus duplex in both, and the presence of a small allanto-chorion in both. The rodents and lagomorphs agree with the primates in the presence of a discoidal deciduate placenta, which is surely parallelism in the latter case. Many authors since Tullberg have felt that the embryologic and reproductive characters are indicative of relationships, but Hartman (1925) considers that the embryologic structures strongly supported Gidley's separation of the Lagomorpha as a distinct order.

Simpson (1945), while accepting the ordinal distinction, still left the two orders together in a Cohort Glires, which he felt was "permitted by our ignorance rather than sustained by our knowledge" (op. cit. p. 196). In this he has been followed by various later authors.

All of the features given above as characters of the Lagomorpha are distinctions from the rodents. Of these, perhaps the most striking is the difference in tooth pattern, there being no present basis even of working out probable homologies between the different parts of the teeth in the two orders. There does not seem to me to be any valid basis remaining at the present time for considering that the rodents and lagomorphs have a common ancestral basis, short of something which would unquestionably be an insectivore. The two lines are independent back to the Paleocene, with no suggestion of greater affinity then than now. The similarities are of two types—those determined by the fact that both are gnawers, and those that merely indicate that both are rather primitive mammals. It should again be stressed that Hartman (1925) considers that the embryologic simliarities between the two orders have been greatly overemphasized, and that the embryologic patterns of the two orders are actually so different that they can be considered as supporting the separation of the Lagomorpha as a distinct order. Serological studies of relationships of the lagomorphs to other orders have not generally been made, since most such studies use the rabbit as a source of sera for making the tests, but

Moody, Cochran and Drugg (1949) have pointed out that there is no serological evidence that lagomorphs are more closely related to any of several rodents than to cow, man or raccoon.

If the rodents should be eliminated as close relatives of the lagomorphs, where can we look for their origins and closest relatives? The situation is unchanged from Tullberg's day—there are still no other groups showing close relationships to either order. There have been a number of suggestions as to specific non-rodent ordinal relatives of the Lagomorpha, but each such suggestion raises as many difficulties as it eliminates.

A rather surprising group—the Mesozoic order of the Triconodonts—has been suggested by Gidley (1906) and Ehik (1926) as related to the lagomorphs, though with quite different emphasis. Gidley illustrated diagrammatically (1906, fig. 12, p. 99) the derivation of the teeth of the Oligocene *Palaeolagus* from those of *Triconodon,* through a hypothetical intermediary. He did not discuss this suggested derivation in any way. However, his diagram indicated that he interpreted the pattern of both upper and lower molars of *Palaeolagus* as being three cusps in an antero-posterior row, an assumption for which there is rather clearly no justification at present (see Wood, 1940, various figures, including figs. 71, 73, 77, 80, 81, 82, 85 and 86).

Ehik's view was that, in the origin of the lagomorphs, "where the process of trituration consists in a transverse movement of the mandibles, the three main cusps of the triconodont type are not disposed longitudinally, but transversely" (1926, p. 182). He does not indicate clearly whether he considers that this represents a rotation of ninety degrees of the triconodont teeth, or whether he is postulating a hitherto unknown group of triconodonts. This description fits the upper premolars of early lagomorphs (for *Titanomys,* see Ehik; for *Palaeolagus,* see Wood, 1940) better than any other description that I have encountered, but it is hard to make this type of a history for the upper teeth accord with the rather typical tuberculo-sectorial lower teeth of lagomorphs. Moreover, while it is perhaps possible that the ancestor of the Lagomorpha had teeth made of three cusps arranged in a transverse row, there does not seem to be any valid basis for referring such hypothetical ancestors to the Triconodonta.

The marsupials have not recently been suggested as the ancestors of the lagomorphs, Schlosser (1884, p. 131) being one of the last to have supported this point of view. Gregory (1910, p. 325) points out the presence of a vertebrarterial foramen in the 7th cervical vertebra of lagomorphs as a marsupial feature, to which could be added the short palate. Matthew, however, (1937, p. 135) shows that some other mammals, notably *Orycteropus,* also have perforate seventh cervicals. Petrides (1950, p. 99) states that only the lagomorphs among the placentals agree with the marsupials in that the scrotum is in front of the penis, rather than behind it. The deposition of albumen around the ovum in the fallopian tube is a marsupial character (Hartman, 1925).

Since the lagomorphs are generally accepted as being eutherian mammals, they are presumably ultimately derived from the insectivores. There does not seem to be any indication that these last gave rise directly to the lagomorphs. Unquestionably, however, the early insectivores did give rise, directly, to a number of gliriform groups, so that the possibility remains that the lagomorphs are one such group. The basic tooth pattern of the Lagomorpha, as discussed below, makes this source rather improbable. On the other hand, it seems very probable that the rodents were derived, through the Paleocene-Eocene stock of the Paramyidae, more or less directly from the insectivores.

The only suggestion of primate relationships for the lagomorphs was the questioned reference of the upper teeth of *Eurymylus* to the Plesiadapidae by Mat-

thew and Granger (1925, p. 7). However, the same authors referred the lower teeth to the Order Glires, which they used as including both rodents and lagomorphs. Later, Matthew, Granger and Simpson (1929, pp. 5–7) associated the upper and lower teeth, assigned both to *Eurymylus*, and referred them all to the Glires. Like the insectivores, the primates have given rise to several gliriform groups, but the lagomorphs do not seem to have been one of them.

There have been a number of attempts to establish relationships between the lagomorphs and the artiodactyls. Cope's (1883) and Gidley's (1912) comparisons have already been mentioned. Hürzeler (1936) pointed out similarities between the Lagomorpha and *Cainotherium*, from the Oligocene and Miocene of Europe. These resemblances include the general size and appearance of the skeleton, the method of chewing by transverse motion of the jaws, the type of locomotion as indicated by limb structure and limb ratios, and the fibular-calcaneal articulation typical of artiodactyls. Since, however, both artiodactyls and lagomorphs are known as early as the upper Paleocene, there obviously can be no special relationships between mid-Tertiary members of the two groups. The most that could be expected is that parallel evolution in the two orders might suggest basic relationships. Serology gives additional support to the possibility of artiodactyl-lagomorph relationships, Moody, Cochran and Drugg (1949) pointing out that, while the serological relationships of lagomorphs and artiodactyls were not close, they appeared to be closer than those of lagomorphs and rodents. Not enough data are available for conclusive demonstration of any special lagomorph-artiodactyl relationship, but the possibility must certainly be borne in mind.

The resemblances between the lagomorphs and the uintatheres and amblypods are at first glance not very obvious. It was not until after I had developed the feeling that there were notable similarities in tooth pattern between the two groups that I learned that J. J. Burke had previously developed the same idea. In both groups, the lower teeth are obviously tuberculo-sectorial, and the upper teeth are peculiar, to say the least. In the lower teeth, the pattern found in *Uintatherium* (Romer, 1945, fig. 293E) shows trigonid and talonid each formed of a lobe, and on some teeth at least, a third lobe behind the talonid, as in *Palaeolagus*. These resemblances are not very close, and at most give a faint suggestion of relationship.

In the upper teeth, however, there are rather striking similarities between molars of *Coryphodon* and premolars of *Palaeolagus* (fig. 1), as pointed out by Wood (1940, p. 358). In both, there is an anterior marginal crest, which runs into a lingual cusp that seems to be the protocone. In both, there is a V-shaped crest forming the postero-buccal part of the tooth, which seems to be made up of the paracone, near the middle of the buccal margin of the crown, and the metacone, near the middle of the posterior margin of the tooth. In both, a crest runs from the metacone to the postero-external corner of the tooth, completing the V. If the analogy of the premolars can be used to interpret the origin of the lagomorph molar pattern, this must be what has occurred here, as well. Perhaps the chief difference between *Coryphodon* molars and *Palaeolagus* premolars (and, perhaps, molars) in the presence of only a single lingual cusp (protocone) in the former, whereas the latter also has a hypocone. Since these two cusps in the premolars of Oligocene lagomorphs are very recent developments, and surely not homologous to the cusps usually given these names, it is not clear how much weight should be given to this difference. There does, however, seem to be a rather striking similarity in the tooth pattern of these forms, suggesting parallelism in their mode of development. It seems unlikely "that these resemblances between the lagomorphs and the coryphodonts are indications of close relationship, but it does

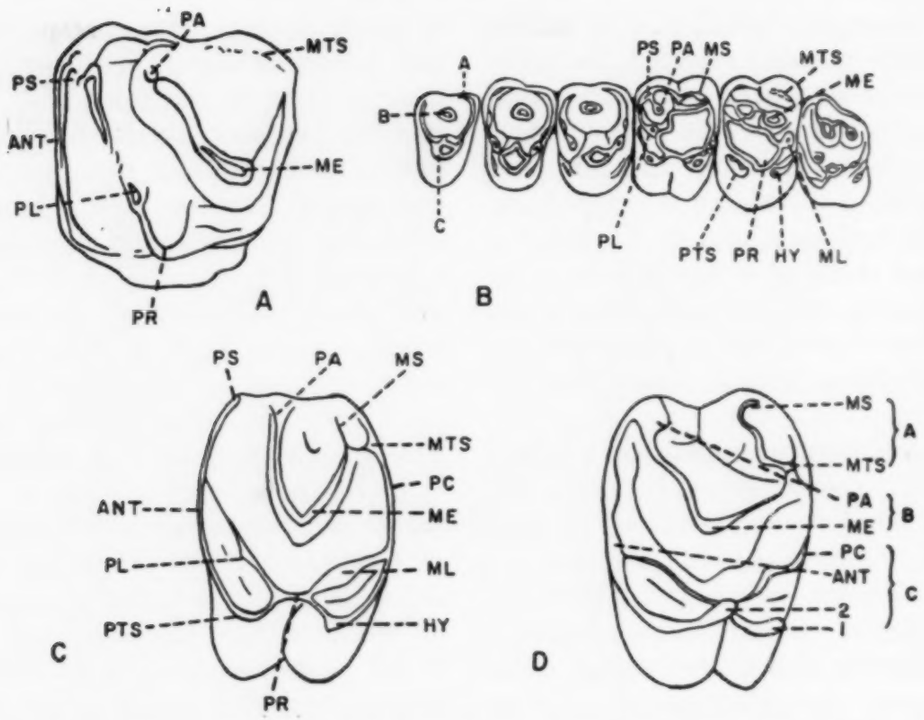

FIG. 1. Comparisons of upper teeth of various mammals, with anterior ends to left. Not to scale. A. *Coryphodon,* upper molar after Simpson, 1929, figure 5 a. B. *Ectoconus,* upper premolars (P^{2-4}) and molars (M^{1-3}), after Matthew, 1937, figure 27. C. *Palaeolagus,* first upper molar, after Wood, 1940, figure 81, reversed. D. *Palaeolagus,* fourth upper premolar, after Wood, 1940, figure 114.

A—External cingulum and its derivatives; B—Amphicone and its derivatives (Paracone and Metacone); C—Protocone and its derivatives; Ant—anteroloph; Hy—hypocone; Me—Metacone; Ml—metaconule; Ms—Mesostyle; Mts—Metastyle; Pa—Paracone; Pc—Posterior cingulum; Pl—Protoconule; Pr—Protocone; Ps—Parastyle; Pts—Protostyle. 1—So-called hypocone; 2—So-called protocone.

seem possible that this might be an indication, in a general way, of the primary mammalian group to which the lagomorphs may belong, since it is well known that parallelism is much more common and perfect among related than unrelated forms" (Wood, 1940, p. 358).

CONDYLARTH ORIGIN OF LAGOMORPHS

The fact that there are similarities between the lagomorphs and artiodactyls and between the lagomorphs and pantodonts and Dinocerata suggests the possibility that all these forms are broadly related, and that the origin of the lagomorphs is to be sought within the great ungulate stock, more specifically, among the Condylarthra. As pointed out by Simpson (1945, p. 234), the Condylarthra include three rather distinct groups, the hyopsodonts, phenacodonts and periptychids, the latter being perhaps most closely related to the pantodonts. Because of the suggested similarity of the lagomorphs and pantodonts, initial comparisons were made between lagomorphs and periptychids.

A periptychid such as the lower Paleocene *Ectoconus* (Matthew, 1937, pp. 128–144; figs. 27–29 and pls. 23–32) possesses a basic tooth pattern which is reminiscent of that of *Palaeolagus.* The lower molars are clearly tuberculo-sectorial and, upon wear, develop two distinct lobes, i.e., the trigonid and talonid. While they are very obviously different from those of the lagomorphs, there would be no great difficulty in deriving the lower molars of *Eury-*

mylus or *Palaeolagus* from those of *Ectoconus*. The lower premolars of *Ectoconus* are definitely non-molariform, and would have a long way to go to be transformed into those of lagomorphs, but there is a considerable time between the Puerco and the Gashato, and the *Ectoconus* premolars are not specialized beyond what could yield a lagomorph. The upper teeth of *Ectoconus,* however, have a number of striking similarities to those of *Palaeolagus* (the upper teeth of *Eurymylus* are too badly worn to permit useful comparison). The molars of *Ectoconus* have large paracones and metacones, placed somewhat lingually and separated from the outer margin of the teeth by large buccal cusps (fig. 1 b). The paracone and metacone are united into a diagonal ectoloph, the metacone being separated from the metastyle of M^{1-2} by a deep basin. The protocone is a fairly large cusp, extending via the protoconule to the anterior margin of the tooth, and via the metaconule to the middle of the posterior margin of the tooth. This, on wear, produces a diagonal dentine area, quite suggestive of the antero-internal portion of *Palaeolagus* molars (fig. 1 c). The two lingual styles are in a position where their accentuation would give a pattern that suggested the splitting off of the hypocone from the protocone, as in *Palaeolagus,* without actually being such cusps. That such a background is a true picture of the origin of this part of the tooth in *Palaeolagus* is suggested by the unworn M^1 of *P. temnodon* (Wood, 1940, fig. 81), diagrammatically reproduced as figure 1 c. In this tooth, as Bohlin (1942, p. 33) points out, the lingual half of the tooth could be considered to represent a protocone, with slight swellings on its arms representing the protoconule and metaconule, with the apex of the protocone at the end of the internal fold, and with anterior and posterior cingula elevated on either side. As he also points out, the posterior cingular cusp would then be a hypocone and the anterior one would not be the protocone, so that the antero-internal buttress of the lagomorph upper molar would have to be a protostyle. This being the case, the only major difference in terminology between Bohlin and Wood in lagomorph upper molars is as to the position of the paracone, the cusp that Bohlin considers to be the paracone apparently not being present in American Oligocene forms. We are, however, in agreement as to the approximate location of the paracone. This interpretation of cusp homologies is indicated on figure 1 c.

The upper premolars of *Ectoconus* (fig. 1 b) have a large amphicone on the buccal half of the tooth; a large protocone on the lingual half; and anterior, posterior and external cingula. The protoconule and metaconule are developing from these cingula on P^{3-4}, and lingual styles are beginning to arise on the posterior premolars, in the same position as in the molars. That is, these premolars are becoming molariform, in apparently the same way that the molars previously did. This is quite different from what is found in lagomorphs. However, the pattern of P^2 is not very far from what Wood (1940, p. 353 and fig. 114) indicated as a starting point for the upper premolars of Oligocene lagomorphs, a tooth with one buccal and one lingual cusp, connected by an elevated posterior cingulum, and with a small buccal cingulum. The sequence of development of the lagomorph upper premolars seems to be as given by Wood (op. cit., fig. 114), which is very different from that followed by the molars, although ultimately resulting in teeth superficially identical to the molars.

This raises the question of terminology for the parts of the lagomorph premolars. Bohlin (1942, p. 34-35) points out that "To be homologous, the cusps (of the premolars) must at least have originated from homologous primitive tooth elements. As far as I can see there are, however, certain indications that the premolars have developed in a way of their own from a simple pattern, after the molars were already far advanced." Subsequently (p. 37) he concludes that the cor-

responding structures of the molars and premolars cannot be homologous. With this point of view, I find myself in complete agreement. It is therefore necessary to use a different terminology for the cusps of lagomorph molars and premolars, or to use the same terminology with different meanings. Neither of these alternatives is satisfactory, but the second is completely unjustifiable, and I have therefore adopted the premolar terminology indicated by figure 1 d.

The anterior teeth of *Ectoconus* are very different from those of the lagomorphs, with three well-developed incisors of uniform size and a larger canine. There is no suggestion, then, of lagomorph tendencies in the anterior teeth.

Comparison of the skeletons of *Ectoconus* and lagomorphs reveal a number of interesting similarities. The tibia and fibula are distinct, as would be expected in a Puercan form, but there is a distinct fibular-calcaneal facet. The transverse processes of the lumbar vertebrae are large, suggesting lagomorphs. In the only known skeleton of *Ectoconus,* the seventh cervical is perforated by the vertebrarterial foramen on one side but not on the other.

That is, here in the periptychid *Ectoconus,* we have an animal that seems to have essentially as close a similarity to the basic lagomorph pattern as could be expected in a non-gnawing animal. Obviously, *Ectoconus* was not a lagomorph, and was a long way from being one. It seems equally obvious, however, that this would be true of any non-gliriform ancestor of the lagomorphs. The time lapse from Puerco to Gashato is such as to have permitted considerable evolutionary change. Moreover, the known eurymylid material does not tell us much about the details of upper tooth pattern or the foot structure. By the time these features are known, it is Oligocene, long after the period when *Ectoconus* was living. The pattern of the upper premolars of *Ectoconus* is such that it seems certain that it is much too advanced to have given rise to the lagomorphs.

However, it seems a reasonable hypothesis that the ancestral stock of the lagomorphs were condylarths, possibly periptychids, and that the lagomorphs separated from their condylarth ancestry not long prior to the early Paleocene. If this hypothesis is correct, the similarities between lagomorphs and artiodactyls or lagomorphs and pantodonts would be merely the expression of the fact that they all had a condylarth ancestry. A condylarth ancestry would also explain the absence of post-Paleocene forms that could be considered to be related to the lagomorphs, since, by the time the Eocene lagomorphs appear, the Condylarthra were either extinct or had evolved into other orders. The essentially complete absence of Paleocene fossils from most of the world could readily account for our lack of knowledge of the stages intermediate between condylarths and lagomorphs, without requiring assumptions of unusually rapid evolution.

Summary

The following points seem reasonable interpretations of the available data:

(1) There is no special relationship between the rodents and the lagomorphs, the resemblances between them involving either primitive placental characteristics or ones related to the development of the gnawing type of dentition.

(2) The Lagomorpha are placental mammals and, as such, are ultimately derivable from the insectivores. The tuberculo-sectorial lower teeth support such a relationship, as do all the other features of the soft anatomy that indicate that the lagomorphs are placentals. There is, however, no evidence for direct derivation from insectivores, an origin which would appear probable for the rodents.

(3) There are a number of similarities between the lagomorphs and various ungulates. These are sufficiently numerous to suggest that the source of the lagomorphs is to be found in some unknown Paleocene or Cretaceous member of the group. The most likely source seems to be in the Condylarthra, perhaps from somewhere near the periptychids. Although the tooth pattern of the lower Paleocene *Ectoconus* shows many lagomorph similarities, it is already too advanced to have given rise to the lagomorphs.

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FERTILITY AND VIABILITY IN INTERGENERIC PHEASANT HYBRIDS

GUNNAR CONRAD SANDNES

Gettysburg College, Pennsylvania

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In spite of the fact that fertility and viability are to a high degree independently determined, they will be considered together in the present report. This procedure is believed to be justified because, as has been abundantly shown by a wealth of empirical data from many groups of animals and plants, both phenomena are measures of evolutionary progress with respect to ancestral affinities and reproductive isolation. In a general way fertility and viability have been found to decrease in interspecific hybridization as the parental forms are progressively more remotely related. Many other measures can be used for such an assay; some of which, including genetical and cytogenetical characteristics, have already been reported (Danforth and Sandnes, 1939; Danforth, 1950; Sandnes, 1954), while additional information including sex-ratios and the genetical and physiological basis of sterility and intersexuality, will form the subject of future contributions.

Some clarification may be desirable in regard to the use of the term "sterility." In this series of birds the most pronounced examples of sterility are those dependent on apparently complete absence of any germinal epithelium. Equally sterile from a functional point of view, but with a slight advance in the direction of fertility, are other specimens in which the germinal epithelium does contain, at least during the embryonic ages, recognizable germ cells which do not develop further. Still less pronounced cases of sterility show well-developed gonads which apparently never produced any mature germ cells or only germ cells which proved to be non-functional. Even individuals with seemingly normal gonads and germ-cell production may give rise to no zygotes at all, to zygotes which fail to develop, or to embryos and young which die prematurely. The final stages are represented by those seemingly normal individuals which present a graded series from what amounts to complete sterility to a high degree of fertility. Thus, fertility may be regarded as the converse of sterility, but it is measurable over only a segment of the sterility scale. The fertility in both sexes is here expressed as percentage of fertile eggs produced. The highest degree of reproductive compatibility (converse of reproductive isolation, Dobzhansky, 1941) is represented by the production of viable hybrids which in turn are fully fertile.

While the present report deals more specifically with fertility data as such it may nevertheless be appropriate to mention briefly the degree of sterility encountered in the hybrids from some of the crosses. In a later contribution it will be shown that meiosis in *Phasianus-Gallus* hybrids rarely proceeds beyond the stage of chromosome pairing in the males, and never beyond that stage in females. Gonad development is also extremely retarded in other respects, especially in females where some actual regression occurs, and general hormone secretion is lacking or extremely slight as evidenced by the status of accessory and secondary sex traits. A few individuals showed evidence of sex inversion. Similarly, females from the F_1 and the first backcross, as well as some from other crosses involving *Phasianus* and *Chrysolophus,* show marked sterility and intersexuality. Strong evidence for sex reversal in some hybrids derived from these genera will be adduced.

Viability is measured in terms of dura-

tion of survival. Hatchability, the capacity of a fertile egg to actually produce a living chick, will be discussed first, followed by a study of the age distribution in embryonic mortality.

Most publications on the fertility and hatchability of intergeneric avian hybrids fail to give any estimations of statistical significance of data presented. In the present work statistical treatment has been restricted to chi-square applications for goodness of fit. In the case of fertility and hatchability percentages, an arbitrary standard has been chosen in each case for comparison. The percentage chosen is the lowest possible which would give a value of P less than 0.01. For convenience the nearest percentage which meets these requirements is selected from the following series: 0, 5, 10, 15 . . . 100 per cent.

Wherever possible the author has tried to keep in mind the ultimate purpose of the work, namely an appraisal of the phylogenetic affinities of the parental forms. In keeping with this aim there has been included, as preliminary to present and future considerations, a brief general account of the parental genera and species, but a detailed description of the external characteristics will be deferred to a later paper.

The Parental Forms

The original forms from which the hybrids were derived are members of the subfamily Phasianinae, a major subdivision of the family Phasianidae. Beebe (1926) has characterized this subfamily as "pheasant-like," and separates it from other phasianid subfamilies by a tail-moult which is centripetal. Delacour, the leading authority on these forms, regards as "Pheasants" only those genera of the subfamily in which "the male possesses altogether a highly specialized ornamental plumage and large size." Those Phasianinae which lack one or both of these attributes he states are named "Partridges" and "Quails," the Pheasants being classified by him as a separate tribe, the Phasianini.

Pheasants are distributed throughout vast areas of Asia, Malaysia and the neighboring islands, and extend somewhat into Europe beyond the Caucasus. A new species recently discovered in the Belgian Congo unexpectedly extends the range of distribution well into Africa. (As is well known, some species have been introduced into Western Europe and North America.) According to the most recent classification (Delacour, 1951), the Phasianini include 16 genera, 49 species and 121 subspecies. The species and their hybrids which have provided the original data dealt with at this time and in forthcoming papers are representatives of *Gallus, Phasianus, Syrmaticus* and *Chrysolophus.*

Genus *Gallus*

The genus *Gallus* is represented by four wild species, all commonly known as Junglefowls. These are:

Gallus gallus (*G. ferrugineus*), the Red Junglefowl
Gallus lafayettei, the Ceylon Junglefowl
Gallus sonnerati, the Sonnerat's or Gray Junglefowl
Gallus varius, the Green Junglefowl

The three last-mentioned species are not subdivided into subspecies, but the first includes five, among which is *G. g. bankiva* discussed extensively by Darwin. In many respects these wild species resemble the domestic form which is almost certainly descended from one or more of them.

According to Delacour (1951), "Junglefowls inhabit in the wild state the warmer parts of Asia: Ceylon, India, Burma, Siam, Indo-China, the extreme south of China, Hainan and Malaysia (lacking in Borneo), extending to the Lesser Sunda Islands. They are also found in many other islands of the Pacific, but it is generally considered for zoogeographical reasons that they have been introduced by

man, no other birds of the Pheasant group existing in these areas."

Our own *Phasianus-Gallus* hybrids were derived from the domestic fowl. It is therefore of particular interest to consider the relationship of this form to the wild Junglefowls. Many authorities regard the Red Junglefowl as the sole ancestor of the domestic fowl whereas others incline to the view that the latter stems from more than a single species. The former view, first proposed by Darwin, has been strongly supported more recently by such outstanding authorities as William Beebe and Jean Delacour. The latter summarizes this view as follows: "It seems certain that all domestic breeds of poultry are descended from the Red Junglefowl (*Gallus gallus*) and that the other three species played no part in originating them. None of their special characteristics, including their very peculiar voices, can be traced, and all the variations in plumage, shape and size remain well within the possibilities of transformation of *Gallus gallus*. The less specialized domestic breeds such as the Red Game, Brown Leghorn, *et cetera*, reproduce exactly the colors of the Red Junglefowl, and all the other colors are but progressive changes from this early plumage."

Interspecific hybrids between Junglefowls, as well as between Junglefowls and the domestic fowl, have been produced by various investigators in support of the theory of an origin from several species (Ghigi, 1916, 1922, 1934; Lotsy and Kuipper, 1922, 1923, 1924; Punnett, 1923; Hertwig, 1936; Hutt, 1949). The reported fertility and viability does not preclude the possibility of a multiple derivation. It also seems very probable to the present writer that trapping and confining wild Junglefowl in prehistoric times was not restricted to any one species or region, that barter favored dispersal and mixing of stocks, that poultry was most likely crossed indiscriminately, and that culling was not intensively practiced.

It may well be that the genes from the Red Junglefowl predominated in the original domestic chicken of southern Asia, but it is felt that genetic factors from other, possibly all, Junglefowl species were included though not necessarily phenotypically evident. It is believed that data of the kind presented here and elsewhere in our publications, will throw some light on the possibility that the domestic fowl could have arisen from more than one species.

Genus *Phasianus*

The genus comprises the so-called true or game pheasants. Commonly segregated into two or three species, it extends over a considerably greater geographical range (fig. 1) than any other genus of the family. *P. versicolor*, limited to the Japanese islands (fig. 1, nos. 28 and 29), is the most distinct unit, widely recognized as a good taxonomic species. Two other species have at times been recognized: (a) *colchicus*, with various subspecies whose ranges are shown in figure 1 (nos. 1–13); and (b) *torquatus*, with ranges in more easterly Asia shown as 15–27. Recently Delacour has pointed out that the subspecies *tarimensis*, inhabiting the valleys and oases of northeastern Chinese Turkestan forms a connecting link between these two supposed species, both morphologically and geographically. This brings Delacour into accord with most other ornithologists, and we may now regard *colchicus* and *torquatus* as a single species with 27 or more taxonomically recognizable subdivisions most of whose ranges are shown in figure 1. All these forms replace one another geographically, and so far as known, all are capable of freely interbreeding to produce completely fertile hybrids.

The feral population of *Phasianus* in the United States consists of individuals showing varying mixtures of characters of the subspecies *P. c. torquatus* and *P. c. mongolicus*, known respectively by the common names Chinese ringnecked and Mongolian pheasants. (The latter is correctly termed the Kirghis pheasant.) In

FIG. 1. Distribution of the races of *Phasianus colchicus.* From Delacour, 1938. It may be noted that according to current interpretations Nos. 1–27 are all included in *P. colchicus.*

such mixed stocks however genes of one or the other subspecies dominate, and the birds are often referred to as belonging to one or the other subspecies. In a strict sense this is obviously incorrect since they are at best genetic segregates. With this in mind the writer will refer to them simply as Ringneck and Mongolian pheasants.

The melanistic form, *P. c.* mut. *tenebrosus,* was first described from European material by Hachisuka (1926) who correctly interpreted it as a mutation. In the wild state it is said to occur in two phases, one much darker than the other. Simultaneous and independent experiments at Cornell and Stanford (Bruckner, 1939; Danforth and Sandnes, 1939) demonstrated that these two phases are explained by the homozygosity or heterozygosity of a single incompletely dominant gene. In the present report these two genotypes are referred to respectively as M/M and M/m mutants.

Genus *Syrmaticus*

The genus *Syrmaticus* as now constituted results from a regrouping of what

FIG. 2. Distribution of the species and subspecies of *Syrmaticus.* From Delacour, 1938. Nos. 1–8 are now included under *Syrmaticus.*

were originally considered three genera (*Syrmaticus, Graphephasianus* and *Calophasis*). Members of the genus are characterized by similar body conformation, excessively long tails which can be spread out horizontally, and a complete lack of fringed feathers so characteristic of the neck and rump of *Gallus, Phasianus* and *Chrysolophus*.

The genus as it now stands includes ten recognizable forms, the distribution of eight of which is shown in figure 2, 1–8.

Genus *Chrysolophus*

The genus, consisting of only two species, *C. pictus* and *C. amherstiae,* is in many respects sharply delimited from other genera by a conspicuous cape. This consists of greatly enlarged, elongated, and more or less truncated feathers which can be spread into a disk-like form during courtship. The terminal and subterminal transverse black bars are so disposed that during display they form a series of concentric circles. In addition to the highly specialized cape, both species have a crest and mantle which are also considerably specialized.

Morphologically the two species differ appreciably in size, configuration, and skin color of the face. Whereas the general pattern of the back, rump and tail-coverts show considerable similarity, a critical examination of the feathers reveals distinctive differences in structural details, and in actual tone.

The ranges of the two species, as shown in figure 3, do not overlap. Within its range *pictus* extends to an altitude of 4,000 feet, whereas *amherstiae* is found between 7,000 and 12,000 feet.

A melanistic mutant, *C. p.* mut. *obscurus,* occurs not infrequently in captivity. Several of these were raised in connection with this work, but not used in the hybridization experiments.

Description of the Crosses

Some earlier data have been reported for the *Phasianus* × *Gallus* cross (Sandnes, 1937; Sandnes and Landauer, 1938; Danforth and Sandnes, 1939). The last publication also contains a description of the intergeneric hybrids between *Phasianus* and *Chrysolophus*. For the sake of completeness these data are included in the present account.

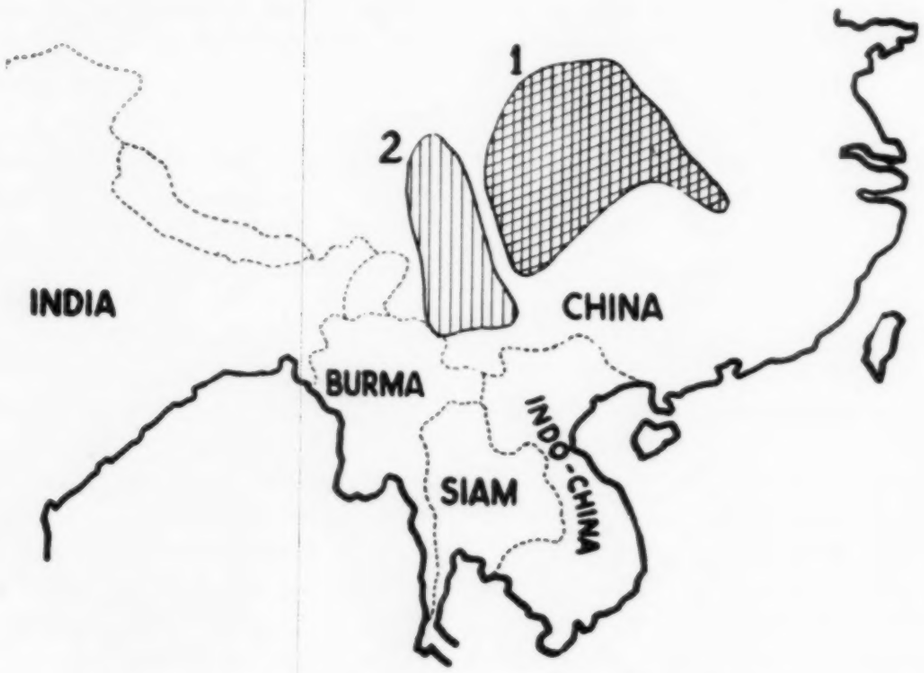

Fig. 3. Distribution of the two species of *Chrysolophus*. From Delacour, 1938.

Intrageneric Crosses

P. c. mongolicus × *P. c.* mut. *tenebrosus*

The early results of this cross have been fully reported in papers by ourselves and Bruckner (Danforth and Sandnes, 1939; Bruckner, 1939). Our own experiments are the outcome of mating a Mongolian male and a mutant female with the production of F_1, F_2 and backcross offspring. One M/m male, No. 125, the son of an F_1 male and a Mongolian female, was mated to No. 88 (below), and produced the four-way hybrid, No. 154, which was the ancestor of our main line of *Phasianus-Chrysolophus* hybrids.

C. pictus × *C. amherstiae*

Reciprocal, F_1, F_2 and backcross matings involving the two species of *Chrysolophus* were made during successive years. An F_1 female, No. 88, resulting from the mating of a Golden male, No. 53, to an Amherst female, No. 28, was herself mated to the Mongolian-mutant male, No. 125, referred to above.

Intergeneric Crosses

Phasianus × *Gallus*

Dr. Walter Landauer in 1936 was the first to use the method of artificial insemination for producing pheasant-chick hybrids. The technique had been developed by Burrows and Quinn (1935) for use by practical poultrymen. The procedure involves the artificial elicitation of an ejaculatory reflex, the collection of semen, and its injection into the oviduct of the female. In my own work Chinese ring-neck hens were inseminated with semen from salmon-breasted white Leghorn males. The hybrids will be discussed in this and succeeding papers.

The reciprocal cross was also attempted, but since it was not possible to obtain sperm from the pheasant artificially, natural matings were resorted to. Although the usual methods for insuring high fertility were employed, e.g., prolonged light, *et cetera,* only two fertile eggs were obtained, one of which died before, the other immediately after hatching.

Phasianus × *Syrmaticus*

Three F_1 hybrids from the mating of a male Reeves pheasant to an heterozygous mutant hen (M/m—from a mutant X Mongolian cross) were obtained. One hybrid, No. 115, was a melanistic female; the remaining two, Nos. 116 and 117, were light in color. The former was lost before maturity, the latter developed as a fertile male. Additional eggs laid by three Mongolian hens mated to a male Reeves pheasant were treated with hormones. One of these hatched into a male hybrid, No. 163, which however had a cerebral hernia.

From 1938 to 1944, hybrid No. 117 was backcrossed to various *Phasianus* and *Syrmaticus* hens. From these matings a number of dead embryos, and chicks which died early in life, were obtained; only two reached adult age. These were both from the backcross to *Phasianus*. One, No. 152, showed the mutant (M/m) pigmentation; the other, No. 181, was "normally" pigmented (m/m).

Phasianus × *Chrysolophus*

As indicated in the section on intrageneric hybrids, all of the *Phasianus-Chrysolophus* hybrids have descended from the mating of a Mongolian-mutant male, M/m, and an Amherst-golden female. From this mating a four-way hybrid male, No. 154, became the ancestor of the main line of *Phasianus-Chrysolophus* hybrids. One other male, No. 155, and three females, Nos. 151, 153 and 162, none of whom left any descendents, were the offspring of the same mother and either the same father or his full brother.

During early generations (F_1 and the first three backcrosses) the female hybrids could not be used for matings because of sterility. In subsequent generations (fourth and fifth backcrosses) some females were fertile and it was then possible to secure offspring which had hybrid ancestry on both sides. (See table 1.)

TABLE 1. *Pedigrees of representative specimens*

Subsequent to B_2 all *Chrysolophus* females used in the following matings were pure goldens. The following twenty-three doubtful specimens, with *Phasianus* blood expressed as parts in 128, are not included in the table: three of 2 or 6 parts; eleven of 4 or 5 parts; eight of 9 or 10 parts; and one of 7 or 13 parts.

Parents		*Phasianus* Parts in 128	*Chrysolophus* Parts in 128	No. reaching 3 mos. of age
Female	Male			
G × B_3	P	66	62	9
C	P	64	64	5
G × B_3	B_4 × P	35	93	1
C	C × P	32	96	3
C	C × F_1	16	112	12
B_4 × B_2	C × B_1	13	115	2
G × B_3	C × B_1	10	118	20
C	C × B_1	8	120	9
G	B_4 × B_2	5	123	8
C	G × B_2	4	124	15
G × B_3	C × B_4	3	125	2
G × B_4	G × B_3	3	125	3
C	G × B_3	2	126	10

From 1939 to 1942, hybrid No. 154 was mated to various *Phasianus* and *Chrysolophus* hens. Only two of his male progeny reached sexual maturity. One of these, No. 179 (C × F_1), although mated repeatedly to both *Phasianus* and *Chrysolophus* females, failed to sire any young. The other, No. 169, however was fertile and was the male ancestor of the remaining backcross generations, B_2 to B_5 and of hybrids derived from these backcrosses. No. 169 hatched in 1939 from an egg laid by a hen of constitution G × A [1] or (A × G) × (A × G), that is, either F_1 or F_2. No. 169 was mated in 1942 to a golden hen and a hybrid of (A × G) × G origin, and sired three fertile sons, Nos. 162, 197 and 198—all of the B_2 generation. No. 198, along with several individuals from later generations, is preserved as a specimen in the Museum of Comparative Zoology at the University of California. Several other specimens from this series may be found in the collection of the California Academy of Sciences. Table 1 shows all the types of hybrids obtained in this series and indicates the proportion of their *Phasianus* and *Chrysolophus* ancestry.

[1] In all formulae the female parent is given first. Other conventions and symbols are explained following the main body of the paper.

FERTILITY AND HATCHABILITY

The two crosses of *Phasianus* × *Gallus* (nos. 1 and 2 in table 2) were effected by artificial insemination while all other crosses were from natural matings. Consequently all fertility values except the first two may be compared with each other. One disturbing factor is the well-known variation in fertility which normally occurs as the breeding season progresses. Some of the pertinent data from *Phasianus* × *Chrysolophus* crosses are presented in table 3. In most cases eggs were collected and incubated throughout the season. Eggs were stored in a cool room for periods not exceeding twelve days before incubation. Hens or for the most part electric incubators were used. A defect inherent in any fertility data is the possibility that the very earliest stages in development may fail to be recognized. All eggs which failed to hatch were opened and inspected.

Hatchability is expressed as percentage of fertile eggs which hatch. It is clearly influenced by incubation conditions, which were kept as nearly as possible constant in regard to temperature, humidity and other requirements. Eggs from the first two

matings were incubated in forced-draft machines. In view of these possible variables only the more marked deviations are discussed.

Phasianus × *Gallus*

Combining the results for crosses 1 and 2 we have 34 per cent fertility and 39 per cent hatchability. The low fertility figure is particularly significant inasmuch as the Quinn-Burrows' technique of artificial insemination ordinarily gives very high values. The inventors of this technique were able to obtain 97 per cent fertility in matings of domestic fowl "differing so greatly in body weights that in natural matings four per cent fertility was the maximum obtained."

A comparison of crosses 1 and 2 is of some special interest because of the ex-

TABLE 2. *Fertility and hatchability in pheasant crosses*

This table is broken down more fully than is needed for the discussion in the text. Female parents are given first. Where more than one female of the same kind was mated the number of individuals is given in parentheses. This does not apply to the *Phasianus-Gallus* crosses where large numbers of females were used for artificial insemination. See list of abbreviations at the end of this publication just preceding the literature cited.

Cross number	Cross	Year	Eggs set	Number fertile	Number hatched	Per cent fertile	Per cent hatched
			Phasianus × *Gallus* Crosses				
1	P_t × Creeper	1936	187	71	13*	38	18*
2	P_t × Leghorn	1937	858	284	124**	33	44**
	1 and 2 combined		1,045	355	137	34	39
			Phasianus-Syrmaticus Male (M/m × S_r, No. 117) Crossed to Various Females				
3	C_p, S_r, M/m × 117	1939	16	2	0	13	0
4	S_r, M/m × 117	1940–42	212	31	5	15	16
5	S_r, P_t × 117	1943	5	0	0	0	0
6	S_r (2), P_t × 117	1944	175	15	1	9	7
	3–6 combined		408	48	6	12	13
			Phasianus-Syrmaticus Male (M/m × 117, No. 152) Crossed to Various Females				
7	M/M × 152	1939	21	0	0	0	0
8	P_m (2) × 152	1940	30	0	0	0	0
9	P_m × 152	1941	?	(all infertile)			
			Phasianus-Syrmaticus Male (M/m × 117, No. 181) Crossed to Various Females				
10	S_r, P_m, G × 181	1943	59	0	0	0	0
11	P_m, P_t × 181	1944	56	0	0	0	0
12	P_m, S_r × 181	1945	62	0	0	0	0
			Chrysolophus Crosses				
13	(G × A) × G	1939	32	24	9	75	38
14	A × (G × A)	1940	18	7	2	39	29
15	A × (A × G)	1939	61	13	1	21	8
16	(G × (G × A)) × G	1940	11	10	2	91	20
17	(G × A) × (G × A)	1939	1	1	0	100	0
	13–17 combined		123	55	14	45	25

* Includes an unknown number assisted from the shell.
** Includes 27 embryos assisted from the shell.

TABLE 2.—*Continued*

Cross number	Cross	Year	Eggs set	Number fertile	Number hatched	Per cent fertile	Per cent hatched
			Phasianus × *Chrysolophus* Crosses				
18	C × F_1 (154)	1939	49	30	6	61	20
19	C × F_1 (154)	1941–42	27	19	8	70	42
	18 and 19 combined		76	49	14	65	29
20	M/m (2) × F_1 (154)	1940–41	98	1	0	1	0
21	P_m × B_1 (169)	1941	28	0	0	0	0
22	G × B_1 (169)	1940–41	36	14	6	39	43
23	G, C × B_1 (169)	1942–43	58	15	14	26	93
	22 and 23 combined		188	58	40	31	69
24	P_t × B_1 (179)	1943	17	0	0	0	0
25	B_2 (small eggs) × (179)	1944	20	0	0	0	0
26	P_d × B_1 (179)	1945	52	0	0	0	0
27	G × B_1 (179)	1946	9	0	0	0	0
28	S_r × B_1 (179)	1947	25	0	0	0	0
29	C × B_2	1941	10	0	0	0	0
30	G × B_2	1941–47	94	65	23	69	35
31	G × B_3	1945–46	105	43	26	41	60
32	G × B_4	1946–47	48	30	20	62	67
33	Hybrids *inter se*	1947–51	297	179	88	60	49***
34	G (3) × (B_4 × B_2)	1948	40	36	28	90	78
35	P_m × B_2	1945	13	0	0	0	0
36	P_w × ((B_4 × B_2) × B_2)	1951	11	0	0	0	0
37	B_4 × P_t	1949	33	28	10	85	46
38	P_t, P_w × (B_4 × P_t)	1950–51	82	0	0	0	0
39	B_4 × (B_4 × P_t)	1950	44	0	0	0	0
40	B_4 (2) × (B_4 × P_t)	1951	35	9	5	26	56
41	P–C (2) × (B_4 × P_t)	1950	27	0	0	0	0
42	P–C × (B_4 × P_t)	1951	18	2	0	11	0

*** Six embryos pipped the shell but did not hatch; these are included among fertile eggs, but not among birds hatched. In addition, seven late embryos were killed, so that hatchability might have been higher.

pression of the creeper gene in the hybrids. Landauer (see his 1948 publication) has shown that heterozygous creepers have a higher *late* embryonic mortality than normal embryos. That the creeper gene shows the same lethality in the hybrids is shown in cross 1: 18 per cent hatchability, as compared with 44 per cent for cross 2. When these figures are tested by the chi-square method their significance is indicated by a value much below 0.01. This is the more interesting because cross 1 shows a higher fertility than cross 2. It also emphasizes the lack of direct association of fertility and viability.

Since the Leghorn is the more "normal" of the two *Gallus* parental types, the writer has tested statistically only the fertility and hatchability data of the second cross for association with some arbitrarily assumed values. Significant P values were obtained when the observed fertility and hatchability values, 33 per cent and 44 per cent, were checked against arbitrarily assumed values of 40 and 55 per cent, respectively. This means that statistically the fertility is less than 40 per cent and the hatchability less than 55 per cent.

A number of hybrid chicks listed as hatched were actually helped from the shell. In the second cross, 27 chicks or about 28 per cent were thus assisted. It is not known whether these chicks were hampered by malposition or by the small size of the *Phasianus* egg.

Yamashina (1942 and 1943) reports

TABLE 3. *Seasonal variation in fertility and viability of hybrids from crosses between* Phasianus *and* Chrysolophus

Data for the years 1946–1950 are here grouped according to calendar months. Matings for the most part involved third, fourth and fifth back-crosses to *Chrysolophus* as well as hybrids crossed *inter se*. Embryos classified as having died early were less than eight days old; those listed as late were more than sixteen days of age.

Month	Number eggs set	Fertile	Died as embryos			Hatched	Killed
			Early	Middle	Late		
April	191	98 (51%)	16 (16%)	1 (1%)	39 (40%)	38 (39%)	4 (4%)
May	249	137 (55%)	19 (14%)	3 (2%)	19 (14%)	88 (64%)	8 (6%)
June	129	41 (32%)	11 (27%)	0 (0%)	16 (39%)	14 (34%)	0 (0%)
July	19	7 (37%)	1 (14%)	0 (0%)	3 (43%)	2 (29%)	1 (14%)
Totals	588	283 (48%)	47 (17%)	3 (1%)	77 (27%)	142 (50%)	13 (5%)

data on the *Phasianus* × *Gallus* cross. Natural matings were used throughout. Data given on pages 236 and 237 of his 1942 publication indicate a fertility of 23 per cent for 197 eggs set in the cross of *Phasianus* female by *Gallus* male. (Tested by the writer against a standard of 35 per cent, P is less than 0.01.) Figures given in the 1943 paper show a fertility of 28 per cent for 164 eggs from all matings of both reciprocal crosses. (Tested against a standard of 40 per cent P is less than 0.01.) In his matings, Yamashina used red-hackled Shamo, black Shamo, and red-hackled Shamo bantam representatives of *Gallus;* his pheasants were of the subspecies *P. c. karpowi*. The reason for our higher fertility values would appear to be found in the method of artificial insemination as compared with natural matings, but this assumption is not supported by the data of Shaklee and Knox (1954) who found still lower fertility and hatchability percentages from crosses involving natural matings and artificial inseminations with pure and diluted semen.

In their work they used Dark Cornish and Silver Cornish females, and the male parents were from the cross Ringneck female by Mongolian male. From 106 hens, a total of 1,409 eggs were assumed to have a good chance of being fertile, the percentage fertility being 3.48 per cent. Of the fertile eggs, 6.12 per cent hatched. From natural matings in the year 1951, 679 eggs gave 2.36 per cent fertility, while in 1952 a total of 223 eggs gave 9.87 per cent fertility. The percentage fertility from artificial matings appears to be even lower: of the three groups listed in their table 1 representing the findings from all matings, the highest fertility percentage was 3.85 from a total of 78 eggs.

Of particular interest in this report by Shaklee and Knox was the evidence presented that some of the fertility was "due to causes other than sperm." They conclude that fertility figures "are thought to be overestimates of the actual amount of fertility produced by pheasant sperm."

Phasianus × *Syrmaticus*

The numbers involved in the F_1 generation were small and not very significant. Of 12 eggs laid eight were fertile and

three hatched, giving 67 per cent fertility and 38 per cent hatchability. Some data for the reciprocal cross reported by Haig Thomas and Huxley (1927) are given in table 4 (where I have taken the liberty of correcting their terminology). No dead embryos are recorded in the second cross, but the authors state that some of their records on dead embryos are incomplete. The hatchability in the first and third crosses combined is approximately 70 per cent. This figure is considerably higher than that found in the *Phasianus* × *Gallus* cross.

Our fertile F_1 male hybrid, No. 117, was mated to various pheasant hens during successive seasons. The eggs from individual hens were not always recorded separately so the data in table 2 give combined results for the hens used in any given year and thus serve as a measure of the male fertility alone. Data for the various matings give a fertility of 12 per cent and hatchability of 12.5 per cent. Hybrids from *Phasianus* and *Syrmaticus* eggs were obtained but none from *Chrysolophus* or *Gallus*. Statistically there was no indication that either fertility or hatchability was different in the two backcrosses.

First backcross males (3/4 *Phasianus*), Nos. 152 and 181, were infertile in all matings. As will be seen later, No. 152 was hypogonadic; No. 181 did show normal courting behavior. The impression is that the F_1 and B_1 hybrids are of low viability and either sterile or of low fertility.

C. pictus × *C. amherstiae*

Crosses of these species are commonly made in aviaries and the results are well known, it being generally assumed that there is no reproductive incompatibility between them. Combining the data from our crosses gives 45 per cent fertility and 25 per cent hatchability. Assuming arbitrary standards of 60 per cent fertility and 45 per cent hatchability, the chi-square test gives a P value which in each case is less than 0.01. This would mean that fertility is less than 60 per cent and that hatchability is less than 45 per cent.

These figures might seem low, but data published by Haig Thomas and Huxley (1927) for twelve crosses of a similar nature give a fertility of 41 per cent based on 1,514 eggs and a hatchability of 39 per cent among 624 fertile eggs. Comparing our own data with those of Haig Thomas and Huxley we get P values of more than 0.3 for fertility and less than 0.05 for hatchability. Accordingly it can be concluded that the fertility percentages are in good agreement statistically, but that the hatchability values probably are not. In any case, and despite the popular view to the contrary, it seems evident from our data and those of Haig Thomas and Huxley that at least some reproductive isolation obtains between the species in question.

Phasianus × *Chrysolophus*

Only 15 eggs from the F_1 cross were incubated. Of these, eight were fertile and five hatched. This would correspond to 53 per cent fertility and 63 per cent hatchability. Haig Thomas and Huxley (*loc. cit.*) report that of 16 eggs set by them two were fertile and one hatched, which result, if not quite so good as ours, is still comparable.

A first-generation hybrid, No. 154, was mated to females of the parental genera.

TABLE 4. *Fertility and hatchability in the cross* Syrmaticus *female by* Phasianus *male*

Cross	Eggs set	Number fertile	Number hatched	Per cent fertile	Per cent hatched
S. reevesi × *P. versicolor*	63	19	13	30	68
S. reevesi × *P. c. formosanus*	36	—	8	—	—
S. reevesi × *P. c. colchicus*	30	10	7	33	70

Table 2 indicates a decidedly higher fertility in the backcross to *Chrysolophus* than to *Phasianus*. Testing for an association of fertility in the two crosses by chi-square obviously gives a P value far below 0.01. Since No. 154 derived equal numbers of chromosomes from both parents (cf. Sandnes, 1954), it might have been assumed that he would be equally fertile with either species. Since he obviously was not, two possibilities suggest themselves. 1. In both genera the W chromosome reacts with homologous autosomes but with different valencies in the two species. 2. The two generic sets of autosomes are in some degree themselves incompatible. The former view is considerably strengthened by a consideration of the general discussion in my next publication dealing with the distribution of the sexes among hybrids from this cross. That a differentially reactive W chromosome is not the sole explanation is supported by the fertility ratio 65 : 1 for the respective backcrosses, instead of 3 : 1 which would have been the maximum difference expected on the basis of the first assumption. It therefore appears that both alternatives must be drawn upon to some extent.

First backcross males, Nos. 169 and 179, were mated to various hens over a number of years. No. 179, a beautiful bird showing vigorous courting behavior, was infertile in all matings (table 2). In 1941 mating No. 169 to a Mongolian hen resulted in 28 infertile eggs. This is in good agreement with the one per cent fertility found in matings of No. 154 to M/m hens. The combined data for crosses involving No. 169 with *Chrysolophus* hens yields a fertility of 31 per cent and a hatchability of 69 per cent. Compared with the data for the backcross of No. 154 to *Chrysolophus* hens, one finds a statistically significant lowering of fertility and more than a doubling of hatchability.

The difference between the F_1 and B_1 may be due to a screening out, first, of inviable gametes and, subsequently, of inviable zygotes, both of which might be expected to result from the increased genetic complexity of the B_1 over the F_1. That is to say, in addition to intrinsically inviable gametes there are presumably still others which while themselves potentially viable, form incompatible unions. This would leave a reduced number of gametes which would be viable and make favorable combinations. These two screenings would thus reduce the number of fertile eggs but at the same time result in a higher percentage of the fertile eggs which hatch.

When the breeding data for the cross No. 22, in which golden hens were used, are compared with those where at least one of the hens was a hybrid, cross No. 23, we find a reduced fertility in the latter as compared with the former (26 per cent and 39 per cent), but almost a doubling of the hatchability (93 per cent and 43 per cent). In terms of chi-square the difference in hatchability is significant, that in fertility doubtfully so. Such differences as really exist may be explained in the manner suggested in the preceeding paragraph.

For the later generations facilities did not permit making crosses in a regular sequence such as would result in a uniformly progressive dilution. It was also of course considered important to mate the hybrids among themselves. The latter procedure leads to great complexity in any formal statement of relationships and undoubtedly to an even greater complexity in the actual distribution of genes. For these reasons it seemed proper to combine data from slightly different crosses under a few headings.

It might be expected that with each successive backcross to the genus *Chrysolophus* there would be an increase in hatchability corresponding to the progressively greater numbers of *Chrysolophus* genes. This view is clearly supported by the results shown in table 5 where data drawn from table 2 are listed to show the results of backcrossing hybrid males to pure golden hens. When data for the first two backcrosses are compared with those from

TABLE 5. *Fertility and hatchability in backcross hybrids*

Cross	Crosses in table 2	Number set	Number fertile	Number hatched	Per cent fertile	Per cent hatched
Golden × B_1	22, 27	45	14	6	31	43
Golden × B_2	30	94	65	23	69	35
Golden × B_3	31	105	43	26	29	60
Golden × B_4	32	48	30	20	62	67
Totals		292	152	75	52	49

the last two, a significant increase in hatchability is found, P being less than 0.01.

From theoretical considerations one might expect a reduction in hatchability when such backcross hybrids are mated *inter se*. Recessive *Phasianus* genes present in the hybrids are necessarily heterozygous, and it might be assumed that many of the hybrids have a number of such genes in common. Crossing would bring some of these genes into homozygous combinations which, in a predominantly *Chrysolophus* environment, would be expected to reduce viability. But contrary to such expectation the hatchabiliy proved to be identical for hybrids bred *inter se* and for backcross hybrids, the actual value in each case being 49 per cent. It may be, therefore, that many of the *Phasianus* genes are also normally present in *Chrysolophus* while others are neutral in respect to viability.

AGE DISTRIBUTION OF EMBRYONIC MORTALITY

Introduction

It seems desirable at this point to examine the variations which occur in embryonic mortality in the parental species and their hybrids. In the embryos of the domestic fowl two peaks of mortality, an early and a more pronounced late peak, were recognized by Payne (1919, 1920). Riddle (1930) reported similar periods for species of pigeons and doves. Undoubtedly specific agencies such as certain lethal genes may increase mortality at other definite periods in embryonic development, but in general most factors resulting in an increased mortality are especially effective at these times.

A particularly important publication by Bronkhorst (1933) will provide somewhat of a standard for comparison with our own findings. Bronkhorst studied the mortality distribution of eggs from high-hatching (above 75 per cent) and low-hatching (below 50 per cent) white Leghorn hens. Eggs from the high-hatching groups showed a much lower mortality in the early peak (approximately 1–8 days) than in the late peak (approximately 17–22 days); while low-hatching hens produced embryos which died with about the same frequency in both periods. Both peaks were higher among embryos from the low-hatching hens.

A high late peak of mortality was observed for ring-neck pheasants (Sandnes, 1937). Data are shown in table 6. Here mortality during the last five or six days of development was about eight times greater than during the first six days. When tested for association with an assumed equality of early and late mortality, the chi-square test indicates a significant difference.

Intergeneric hybridization in birds is known to reduce hatchability, and it might therefore be expected that such hybrids would have an increased early mortality when compared with a pure species. This is well supported by data in the literature. Two intergeneric crosses in which the parental forms (domestic fowl × turkey and domestic fowl × guinea fowl) were from different taxonomic families or subfamilies showed an extremely high degree of early embryonic mortality.

TABLE 6. *Mortality of embryos in eggs of ring-neck and ring-neck* × Gallus

Mating	Number fertile	Days of survival			Chicks hatched
		1–6	7–16	17–22	
Ring-neck × creeper	71	45	1	12	13
Ring-neck × Leghorn	284	96	11	53	124
Above combined	355	141	12	65	137
Ring-neck × ring-neck	292	12	9	95	176

Combining the results from both reciprocal crosses in which the turkey was involved (Warren and Scott, 1935; Quinn, Burrows and Gyerly, 1937) it appears that 61 fertile eggs showed a mortality of 98.5 per cent during the first six days of incubation, 75.5 per cent being on the first day. One reached a late stage of incubation, but none hatched. Owen (1941) found that in the cross of chicken female by guinea fowl male all embryos died early, approximately half before the appearance of blood islands, the remainder not later than the fourth day. In the reciprocal cross, early embryonic mortality was again high, but a few survived to late stages and one hatched.

Phasianus × *Gallus*

Data for this cross have already been reported (Sandnes, 1937), but the analysis will be somewhat extended here. Table 6 shows that early mortality is greater than late mortality for both crosses of ring-neck by domestic fowl. In both instances the difference in early and late mortality was found to be statistically significant.

We have already seen that eggs from the ring-neck × creeper cross had a significantly lower hatchability than those from the cross ring-neck by Leghorn. Are the differences in early and late mortality in the two crosses also significant? The value of P in this case is just slightly less than 0.05 indicating a possible significance.

In order to compare the mortality peaks in the hybrid and ring-neck pheasant embryos, data have been expressed as percentages of total embryonic mortality in table 7. It is seen that early mortality in the hybrids is six to eight times greater than in pure ring-necks, and that late mortality in the hybrids is less than half that occurring in the parental forms.

The definite increase in total and early embryonic mortality in this intergeneric cross is most probably the result of abnormal developmental processes induced by the inharmonious interaction of genes from the two genera. On this basis one would expect to find morphological evidences of anomalous development. While no particular attempt was made to study this problem, a very high incidence of cerebral hernia was found. Of 150 embryos and chicks obtained from the cross of ring-neck by Leghorn, 148 were examined for cerebral hernia. This abnormality was

TABLE 7. *Distribution by age of embryos dying before hatching*

(The data in table 6 expressed as percentages of total embryonic mortality.)

Mating	Number of dead embryos	Per cent dead during days		
		1–6	7–16	17–22
Ring-neck × creeper	58	77.6	1.7	20.7
Ring-neck × Leghorn	160	60.0	6.9	33.1
Above combined	218	64.7	5.5	29.8
Ring-neck × ring-neck	116	10.3	7.8	81.9

present in 50 cases—about one-third of the total. Of these, 35 showed protrusion of the cerebrum and meninges while 15 or more exhibited a marked convexity of the crown of the head. Many of the chicks with hernia, although they had to be assisted from the shell, later became physically vigorous.

A high incidence of head abnormalities has been reported by Marchlewski (1936, cited by Landauer, 1948) among embryos from the cross guinea hen × domestic cock. Similar gross structural abnormalities of the head region have also been reported by Owen (1941) for embryos from the reciprocal crosses of the same two species. He states that the "frequency of these abnormalities may indicate a developmental imbalance which finds [even] more consistent expression in other phases of embryonic metabolism, and which is responsible for the high percentage of dead embryos."

Phasianus × *Syrmaticus*

A few data were obtained from matings of F_1 male hybrid No. 117 to *Phasianus* and *Syrmaticus* hens. Records of eggs from the two genera were not always kept separate so that the few data available will be grouped. Of 38 embryos dying in the shell 18 were young, five in the middle period, and 15 late. Early and late mortality are about equal. As in other crosses one might expect a lower mortality in the B_1 generation than in the F_1.

Phasianus × *Chrysolophus*

The distribution of embryonic mortality among backcross and *inter se* hybrids further supports the hypothesis that inharmonious interaction of genes is responsible for the high incidence of total and early embryonic mortality. Successive backcrossing increases the number of *Chrysolophus* genes, and, as has been seen, is associated with an increase in hatchability.

Data from the various crosses will be compared in which the resulting hybrids are presumed to have a low and a high number of *Chrysolophus* genes. For this purpose the data are divided into two groups (table 8). Groups I includes embryos which would not be expected on the average to have more than 15/16 *Chrysolophus* genes. Group II includes embryos expected to have a greater number of such genes. Embryos classified as having died early were less than eight days old while those listed as having died late had attained more than sixteen days of incubation age. Uncertain data are excluded. It is seen that early and late mortality are about equal in Group I while in Group II late mortality is almost double the early mortality. Chi-square tests applied to the data for the two groups indicate only a doubtful significance.

TABLE 8. *Distribution by age of dead embryos among hybrids with low and high numbers of* Chrysolophus *genes*

Crosses	Number of eggs fertile	Number which died			Number hatched
		Early	Middle	Late	
Group I (less than 15/16 *Chrysolophus*)					
Backcrosses	79	26	4	18	31
Complex crosses	88	14	0	15	59
Totals	167	40	4	33	90
Group II (more than 15/16 *Chrysolophus*)					
Backcrosses	66	6	1	17	42
Complex crosses	158	19	0	26	113
Totals	224	25	1	43	155

However, when the data for the two groups are restricted to backcross hybrids a possibly significant difference is found, P being less than 0.02.

Discussion

One of the primary objectives in this study was to get further light on the systematic relations of the species studied. While in a general way our findings tend to sustain those of professional systematists, they nevertheless provide numerous supplementary effects and in one way or another strengthen or weaken current concepts. One point not especially emphasized by systematists but made much of by fanciers and some laboratory students is the supposed complete fertility of crosses between *Chrysolophus pictus* and *C. amherstiae*. If there were a complete lack of sterility barrier between these two forms, those persons who are disposed to consider them as merely of subspecific status would have some grounds for their contention. It might be pointed out, however, that despite Dobzhansky's emphasis on the evolutionary significance of these sterility barriers, geographical isolation alone might produce species wholly distinct as long as they are not brought into juxtaposition. This has been advanced as an explanation for the *Chrysolophus* situation in which two groups of birds differing in size, bony structure, bodily configuration and temperament, to say nothing of differences in every feather, have been thought to be completely fertile. Analysis of our own data and that in the literature from the present point of view goes a good way toward clarifying this situation . It would appear that as a matter of fact some sterility barrier is present, and that these two forms are well on the way to meeting every criterion for a good species; that the F_1 females are prevailingly fertile may be interpreted as merely representing a lesser degree of the sterility expressed even in many intergeneric crosses where the females are not fertile but some of the males are.

Whatever the conception of a genus may be, probably no one could be found who would maintain that *Phasianus* and *Chrysolophus* are of the same species, and yet when intercrossed they produce some fertile male hybrids. This in itself discounts the infallibility of hybrid sterility as an absolute criterion of specific distinctness. From this point of view it seems to us that we are fully justified in recognizing *C. pictus* and *C. amherstiae* as distinct species; species, however, in which the sterility barrier is less highly developed than in the other groups studied. The validity of the other species discussed in this publication is generally recognized and the confirmatory data derived from the experiments need not be reviewed here.

We made no successful crosses between *Chrysolophus* and *Syrmaticus*, but according to Yamashina (1943) who studied some F_1 hybrids, the females are hypogonadic and totally sterile while the testes of the male contain some spermatozoa which are mostly abnormal in form, less than 15 percent of them being normal in appearance. It is thought that such males are either sterile or extremely infertile. In our experience on the other hand both of these genera cross fairly readily with *Phasianus* so that on the basis of the grades of sterility alone the sequence of phylogenesis might be assumed to be *Chrysolophus* → *Phasianus* → *Syrmaticus*, or *vice versa*. Or again it is conceivable that *Phasianus* is the more primitive, *Chrysolophus* and *Syrmaticus* being two genera which have diverged in different directions. Morphological considerations would favor the latter alternative. Coming now to the *Phasianus* × *Gallus* cross, both morphology and sterility indicate relationships more remote than those between either of the other genera.

Considering all the genera together we might picture a phylogenetic tree in which *Callus* was first to become distinct from the other three genera, followed by divergence of *Syrmaticus*, and shortly after the separation of *Phasianus* and *Chrys-*

olophus from the primordial *Phasianus* stem. Each of these genera has diverged to produce several species, and in the case of *Phasianus* and *Gallus* many subspecies. *Chrysolophus* has only two species, and these we may infer, in spite of many morphological differences, are only now in the process of becoming fully distinct. The taxonomic species of *Phasianus,* namely, *P. colchicus* and *P. versicolor* or the older taxonomical groupings (*colchicus, torquatus* and *versicolor*), probably cannot be regarded as good species, but might possibly represent at best something equivalent to the various races of man, and in terms of speciation only potentially incipient species. There is thus represented among the various genera and their sub-groups a wide range of degrees of phylogenetic discontinuities.

From Darwin on there has been much discussion on the origin of the domestic fowl, some contending that it arose from a single species, others maintaining that several species contributed to its origin. Our own experiments are believed to throw some light on problems of this kind. After a certain number of generations, individuals involving two genera and three species, not to mention one other variety, have been produced which are fertile when crossed *inter se*. There still remains considerable sterility as expressed in many intersexes, but it may be presumed that if some of our complex new forms had occurred in nature and proved to have any selective value, a perfectly new species might have arisen.

Interesting evidence for the latter possibility has recently been supplied by Yamashina (1948) for a species of duck, *Anas oustaleti,* which, on the basis of many plumage and other traits, appears to have been derived, by natural hybridization, from two closely related extant species. In this instance the traits analyzed are fairly conspicuous, but it may well be that in many other recent animal species the hybrid origin is much less apparent.

Another aspect of the problem of phylogeny and relationship of these species involves genetic considerations which in turn may be subdivided into the sterility (and relative viability) that results from hybridization and the break-up of genetic complexes that had been established with the species themselves. We have seen evidence of such a break-up in the text of this report, chiefly as a reduction in fertility and viability, the latter being most pronounced at early embryonic ages. Additional evidence of such genetical disruptions will be dealt with in future papers on sex-ratios and the genetical and physiological basis of sterility and intersexuality. The latter contribution will include a general discussion of the mechanisms which appear to operate in the hybridization process and to be determinative in speciation.

Summary

Interspecific and intergeneric hybrids were obtained between *Chrysolophus pictus* and *Chrysolophus amherstiae, Phasianus colchicus* and *Gallus domesticus, Phasianus* and *Syrmaticus,* and *Phasianus* and *Chrysolophus.* In the latter case, especially, the F_1 and subsequent generations were backcrossed repeatedly to *Chrysolophus,* and finally bred *inter se.*

All of the primary intergeneric crosses made produced viable young in appreciable numbers. In the *Phasianus* × *Gallus* cross these young were all sterile, and there was a marked differential viability. In each of the other combinations some fertility was shown by the males but no females until after backcrossing for several generations. In the case of *Chrysolophus pictus* and *C. amherstiae* there was evidence of only minor genetic incompatibility. As more and more *Chrysolophus* blood was introduced into the *Phasianus-Chrysolophus* complex, the females became more and more fertile until it was possible to breed the hybrids *inter se.* Birds with hybrid ancestry on both sides combine traits of the parental genera in varying combinations (Danforth and sandnes, 1939; Danforth, 1950; Sandnes, 1952 and future publications), and it is presumed that one or more distinctive new

types could be derived from this complex material.

A reduction in fertility and an increase in total and early embryonic mortality was found to occur in all the intergeneric crosses studied. This phenomenon was most marked in the *Phasianus* × *Gallus* cross and least in the *Phasianus* × *Chrysolophus* cross. In the former there was a difference in the results depending on whether the *Gallus* parent was a creeper or a Leghorn. There is evidence that the semi-lethal creeper gene has an even more deleterious effect when associated with *Phasianus* genes than with those of the normal fowl.

Both total and early high embryonic mortality so characteristic of first generation intergeneric hybrids was found to be reduced by backcrossing to one of the parental forms.

Our own data on fertility and hatchability when combined with those in the literature indicate that, contrary to general belief, there is a weak sterility barrier tending to separate the two species of *Chrysolophus*.

It is suggested that a satisfactory phylogenetic tree of the four genera considered would show *Gallus* branching off appreciably earlier than the rest, with *Syrmaticus*, and soon after *Chrysolophus*, separating from the *Phasianus* group.

Evidence is presented for the theory of the origin of the domestic fowl from more than one species.

Acknowledgments

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List of Abbreviations

A Amherst pheasant
B_1, B_2 . . . First, second . . . backcross generations
C *Chrysolophus*
c *colchicus*
G Golden pheasant
M Dominant gene for melanism occurring in *Phasianus*
m The presumed allele of M in *Chrysolophus*
P *Phasianus*
P_m *Phasianus colchicus mongolicus*
P_t *Phasianus colchicus torquatus*
P_w A recessive white Mongolian pheasant
S *Syrmaticus*
S_r *Syrmaticus reevesi*

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COMMENTS ON THE WEST INDIAN HONEYCREEPER OR BANANAQUIT FROM GRENADA AND ITS NEAR RELATIVE ON ST. VINCENT

S. Dillon Ripley

Yale University, New Haven, Connecticut

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Among a collection of birds from Grenada, British West Indies, obtained through the kindness of Mr. W. J. Plowden-Wardlaw, are twenty-eight specimens of the polymorphic Bananaquit of that island, *Coereba flaveola aterrima*. This population exists in two forms, a normal phase, resembling other West Indian and Neotropical Bananaquits in being dark above with a pale yellowish rump, white superciliary, and mostly yellow below with a dark gray throat patch and greenish olive flanks. This is the form which was called *Coereba wellsi*, normal form *morrisi*, by Clark (1905) Proc. Boston Soc. Nat. Hist., **32**: 293), and which he reported was "very rare" on Grenada; "seen but twice on the mangrove flats of Point Saline."

This phenotype more nearly resembles *C. f. luteola* of Tobago, Trinidad and northeastern South America, than the other adjacent island populations of normal Bananaquits, differing, however, in possessing a tumid, bright pink rictal spot, and in having a much darker throat patch, and a duller rump patch.

The melanistic phenotype, the type of the name *aterrima*, is virtually completely black, except for a tendency to paler inner edges to the inner secondaries, a greenish olive tint to the rump, and an oil green tint to the slate-colored feathers of the breast.

Immature birds of the normal type tend to have dull brownish upperparts, sometimes spotted with new black feathers, the superciliary partly or predominantly yellow, and lack a throat patch, the whole of the underparts being dull yellow, with sooty bases to the throat feathers.

The immature of the melanistic phase is dull, blackish-brown above, paling to an oily yellow suffusion on the dull, brownish rump, and dull, clove brown below, washed with olive green.

Apparently the rare occurrence of normal birds among the otherwise melanistic population is confined to two areas on the Island of Grenada (see accompanying map, fig. 1); in the extreme northeast in the Levera area, near Levera Island, Green Island and Sandy Island, and in the southwest, at Point Saline, and near it, on "True Blue" Estate. This distribution has been noted by previous collectors going back into the Nineteenth Century, and from the meager comparative evidence, it would appear that this is a balanced condition of polymorphism, not transient, as Bond has pointed out (1956). Thus all 'round the Island and wherever it may occur in the interior, the Bananaquit is black. Only at these two discrete points, northeast and southwest, do normal type birds appear, and in general it might well be asserted that they are as uncommon now in these days of better transportation and facilities for field study, as they were in the days of Clark (*op. cit.*) or even earlier. This evidence is in contrast to the assumption of Huxley (1942) and earlier writers (Meise *et al.*), that the situation was in imbalance, and that the melanistic phase was replacing the normal phase.

In size and tone of coloration, melanistic birds from all over the Island appear similar. There is no difference in color between normal specimens from Point Saline and Levera, or Islands to the north including the near-by Green Island, al-

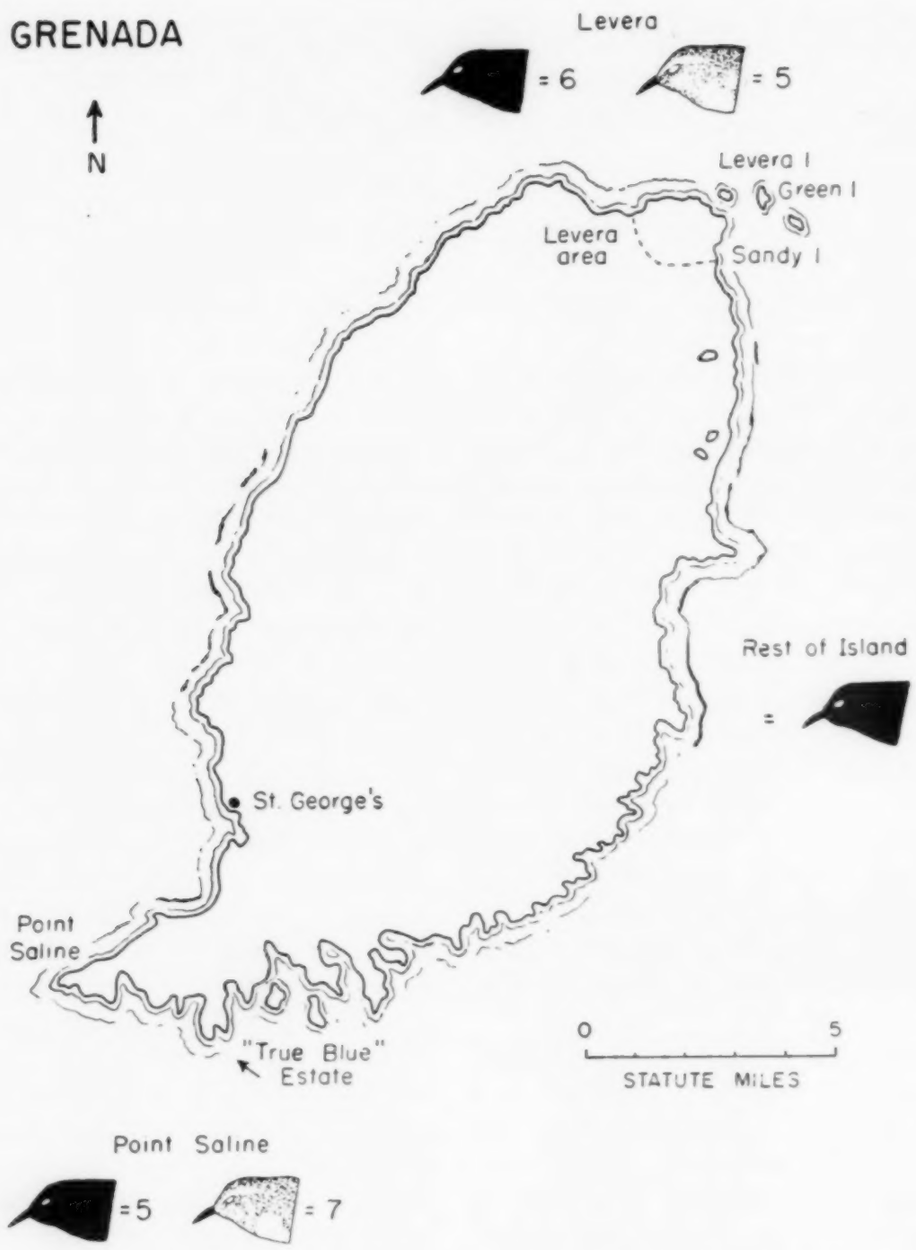

FIG. 1. Map of island of Grenada showing distribution of Honeycreepers.

though there is a small but appreciable cline in size. However, the population of the Grenadines and Green Island seems to consist only of normal individuals. It might be speculated that Grenadines birds serve as a reservoir or gene pool from which to reintroduce the normal phase to Grenada at intervals, due to the proximity of the Islands to the Levera colony, were it not for the persistence of the isolated Point Saline colony far to the southwest.

This is a discontinuous form of geographical variation, St. Vincent to the north, north of the Grenadines (fig. 2), has a larger-sized subspecies, primarily melanistic, with occasional normal individuals occurring, and the islands to the southwest, off the Venezuelan coast, have three taxonomically separate melanistic populations.

Mr. Plowden-Wardlaw comments (in litt.) that the Levera Colony of mixed type is very small; "only 500 yards long along the beach, amongst the sea grapes and almonds, and only a few hundred yards deep."

A curious point brought out in his collecting, and one which he feels represents the presence of a possible sex-linked character among the Levera colony of mixed types, is that the sex ratio is unequal as between the two types:

Specimens collected by Plowden-Wardlaw	Normal	Melanistic
Levera area	4♂♂	2♂
	none	4♀♀
Additional Specimens in Harvard Museum of Comparative Zoology and Philadelphia Academy of Natural Sciences	1♂	
Point Saline area	2♂♂	1♂
	3♀♀	4♀♀
Additional Specimens at MCZ and ANSP	1♂, 1♀	

Mr. Plowden-Wardlaw suggests that the mixed pairs which he collected at Levera demonstrated that the two plumage phases were sex-linked, normal males being mated to melanistic females. It would be interesting to attempt to test this hypothesis, which unfortunately is difficult by the method of simple collecting, and which the presence of two males among the melanistic series collected tends to discredit.

Since there is a total of seven normal and five melanistic specimens from Point Saline and five normal and six melanistic from Levera, making in all twelve normals and eleven melanistic specimens, it is possible to conclude that the approximate gene frequency, assuming equilibrium, is not significantly different in the two localities. It is possible to assume also, therefore, in an approximate way that the two phenotypes occur in equal proportions. For an equilibrium mixture of equal numbers of two phenotypes, differing in a single gene with no phenotypic difference between dominant heterozygote and homozygote, the proportion of genes is 71% recessive, 29% dominant as Dahlberg has shown (1948).

	Measurements (in millimeters)	
	Wing	Tail
Levera, Point Saline, Grand Anse, "Grenada" Total of 12♂♂♀♀ normal:	55.5–63.5 (mean 59) $\sigma_m = 2.62 \pm .79$	33–40 (mean 37.1) $\sigma_m = 2.26 \pm .75$
Levera and Point Saline 6♂♂♀♀ melanistic:	57.5–62 (59) $\sigma_m = 1.682 \pm .68$	34–38.5 (36.4) $\sigma_m = 1.79 \pm .07$
Rest of Island, St. George's Beau Sejour, St. Paul's, Calavini, Grenville, Morne Rouge, "Grenada" 13♂♂♀♀ melanistic:	52–60 (56.5) $\sigma_m = 2.417 \pm .78$	28–40 (33.3) $\sigma_m = 3.81 \pm 1.27$

From the above figures it will be seen that the size of the normal and the melanistic birds from the areas where the normal persists in the northeast and southwest of the Island is closely equivalent. Melanistic birds from other parts of the Island where only this phenotype occurs average slightly smaller. Comparing the means of the wing measurements of the melanistic samples from the Levera and Point Saline loci with those from the rest of the Island by the formula of t for small samples reveals a t value of 2.05 which gives a probability between 1.8 and 2.1. Similarly the t value for the difference of the means of the tail measurements between the melanistic samples is 1.9 which gives a probability near .10. On the basis of this evidence the probability is not great that the samples represent discrete populations. However, it cannot be entirely overlooked that there is a slight

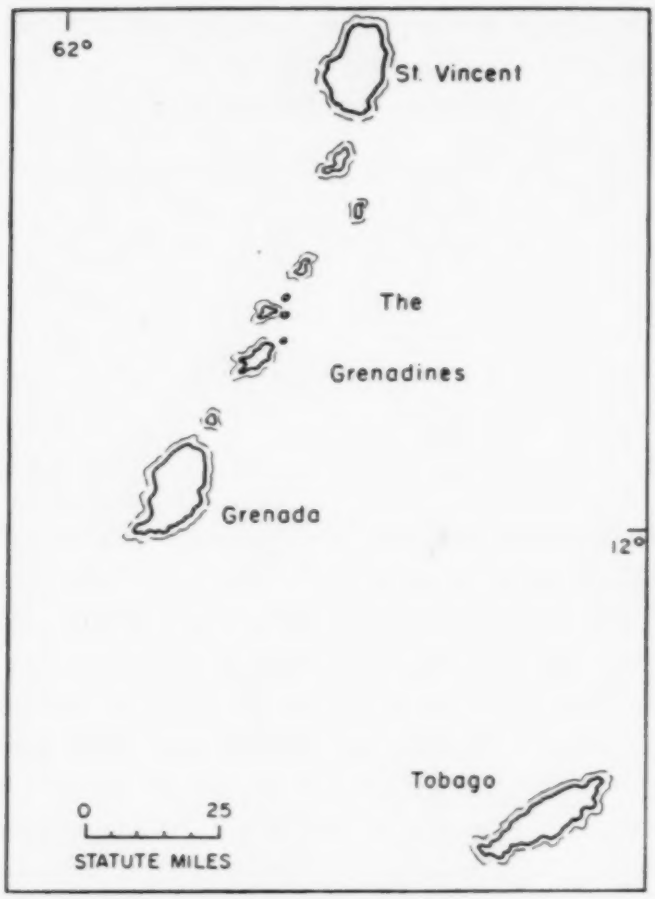

FIG. 2. Map of islands in vicinity of Grenada.

trend towards larger size in the polymorphic populations.

Thus the Grenada Bananaquit does appear to represent a case of balanced polymorphism with two isolated geographical loci, in each of which the normal type apparently interbreeds freely with the melanistic type, and in each of which a random sampling reveals a trend towards larger size.

ST. VINCENT AND THE GRENADINES

The Grenadines Islands north of Grenada are inhabited by a normal population of Bananaquit which is indistinguishable from *aterrima*. Specimens seen by me measure: 8♂♂♀♀; wing 55–63 (59.7); tail 32–38 (35).

Birds from St. Vincent have been named *atrata* and are said to differ from *aterrima* by larger size, more robust bills, and deeper color in the melanic specimens. Direct comparison of specimens has not satisfied me that the characters of more robust bill or deeper color in the melanistic birds were in themselves significant. The normal specimens are in fact indistinguishable. It seemed worthwhile then to examine the alleged variation in size. Specimens of normal and melanistic type combined measure: St. Vincent, 8♂♂♀♀; wing 57–64.5 (62); tail 32–42 (37.5).

Adding the Grenadines sample to that from Grenada gives a total of 27 specimens with measurable wings ranging in size from 52–63.5 with a mean of 58.4 mm. Comparing this sample with 8 St. Vincent birds as measured above, gives a figure for $\sigma_d = 1.26$ and $d/\sigma_d = 2.85$. This figure when arranged on a normal curve table indicates that the probability is highly significant that the St. Vincent specimens do in fact represent a separate population. Thus even though individual St. Vincent or Grenada birds may overlap in size and be otherwise inseparable, it seems wiser to assume that two genetic populations are here represented, and that these populations are significantly isolated, and in both a condition of polymorphism occurs. Here again it seems particularly noteworthy that the geographically intervening population on the Grenadines, which in size appears to belong with that of Grenada, is entirely composed as far as is known of normal phenotypes.

I am much indebted to Professor G. Evelyn Hutchinson for looking over these notes, and to the authorities of the Philadelphia Academy of Natural Sciences and the Harvard Museum of Comparative Zoology for permission to examine specimens in their care as well as to Mr. J. D. Macdonald of the British Museum for measurements of additional specimens.

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THE POLLINATION OF *PARKIA* BY BATS AND ITS ATTENDANT EVOLUTIONARY PROBLEMS

H. G. Baker and B. J. Harris

Department of Botany, University College of Ghana, Achimota, Ghana

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Introduction

Cheiropterophilous plants are pollinated by bats which visit their flowers. This process is peculiar to species growing in tropical regions where suitable vegetarian bats occur. Relatively few systematic and sustained investigations of the process have been made and it is the aim of this paper to provide first-hand observations upon the bat-pollination of a species of *Parkia* (Mimosaceae) and to discuss the evolutionary problems which they raise.

The first suggestion that bats might act as pollinating agents for flowering plants was made by Moseley (1879) who observed bats attacking and eating the red flowers of a tree, probably a species of *Erythrina* (Papilionaceae), during the hours of daylight. These observations were made in the Pacific islands of Tonga during the cruise of H.M.S. Challenger. This record was not, however, the first to be made of bats visiting flowers, the honor for which probably belongs to De La Nux who, in a letter dated 1772, wrote to the French botanist Buffon that he had seen bats of the species *Pteropus niger* visiting flowers of an unknown "umbelliferous" plant at Reunion in the Mascarene Islands (Jaeger, 1954b). Subsequently, Gould (1863) in Australia, saw flowers of *Eucalyptus* attacked and eaten by *Pteropus alecto gouldi*.

After Moseley's publication, further observations of flower-visits by bats were made in Trinidad by Hart (1897) who recorded visits to *Bauhinia megalandra* Griseb. (Caesalpiniaceae). Hart, in a letter to Knuth (cited by Knuth, 1908), also recorded visits by the bat now known as *Anoura geoffroyi* (Peters) Gray to the flowers of *Eperua falcata* Aubl. (Papilionaceae). At Buitenzorg (now Bogor) in Java, Burck (1892) reported that the bat *Pteropus vampyrus* (Linn.) Brisson paid attention to the flowers of a liane which was finally identified by van der Pijl (1956) as *Freycinetia insignis* Bl. (Pandanaceae). Confusion has arisen regarding this work by Burck because other species of *Freycinetia* are bird-pollinated.

Again, at Buitenzorg, Heide (1927) was the first to observe *Eonycteris spelaea* Dobson, a small fruit bat, visiting the flowers of planted specimens of *Kigelia aethiopica* Decne. (Bignoniaceae) and *Markhamia* (*Dolichandrone*) *stipulata* Seem. (of the same family). In India, McCann (1931) described the behavior of the bat *Cynopterus sphinx* Vahl. which visited the flowers of *Kigelia pinnata* DC. and *Oroxylon indicum* Vent. (again of the Bignoniaceae).

A second record from the New World was made by Porsch (1931) who observed visits in Costa Rico by *Glossophaga soricina* Pall. to two species of Calabash tree, *Crescentia cujete* L. and *Parmentiera alata* Miers. Once again the species visited belong to the Bignoniaceae.

In 1936, Altmann informed van der Pijl (1936) that he had observed small bats visiting the flowers of the Baobab (*Adansonia digitata* L., of the Bombacaceae) planted in Java, but it was not until 1943 that Jaeger (1945) confirmed this from French West Africa where the species is native. Jaeger observed visits by the large fruit bat *Eidolon helvum* Kerr to this tree. Subsequently, Jaeger (1954a) published his description of the visits of an unidentified bat to the Silk Cotton Tree (*Ceiba pentandra* Gaertn., also of the Bombacaceae) in the same region.

Van der Pijl (1956) published the first photograph of a bat visiting the male flowers of *Musa paradisiaca* L. (Musaceae). Since this species produces fruits parthenocarpically, the visits of the bat (which was a species of *Macroglossus*) have no significance for pollination.

Visits by bats to flowers of the genus *Parkia* were first observed at Buitenzorg by Danser (1929) on the species *P. speciosa* Hassk., now known as *P. roxburghii* G. Don. In the same year, van Heurn (1929) reported that as long ago as 1926 he had shot specimens of the bat *Cynopteris brachiotis* Muller on this same species of *Parkia*. Docters van Leeuwen (1933) gave an account of his observations made in 1932 on *P. roxburghii* at the same locality in Java, but referring to another species of bat, *Eonycteris spelaea* Dobs.

In the early writings there is much discussion as to whether the bats are simply destructive. Gould (1863) states that the flowers of *Eucalyptus* were eaten and Moseley (1879) found the same in *Erythrina*. Similarly, Porsch (1951) and Cammerloher (1928) were of the opinion that the visits to *Freycinetia* recorded by Burck (1893) were purely destructive and that the bats were the cause of the rarity of fruiting in *Freycinetia* at Buitenzorg. Hart (1897) noticed that immediately after a flower of *Bauhinia megalandra* Griseb. had been visited by a bat, the corolla fell to the ground.

In general it would appear that bats visit flowers for food in the form of nectar, pollen, or the floral parts. The greatest physical damage to the floral parts is done by those bats which eat the corolla, but the loss of the corolla does not necessarily mean that pollen has not been transferred to the stigma and seed-setting is not ruled out. Danser (1929) observed that the stamens of *Parkia roxburghii* had been gnawed off by bats, but that the tree produced large numbers of fruits. It seems that there is a range of behavior between that of the extremely destructive visitors and those which effect pollination without damage ("ravageurs" and "pollinateurs," respectively, of Jaeger 1954b).

Despite the wide geographical range over which bat visits to flowers have been recorded (the West Indies and Central America, West Africa, India, the East Indies, and Australia) and their attempted survey in review articles by Jaeger (1954b) and van der Pijl (1936, 1956), there remain many gaps in our knowledge of bat-pollination both from the point of view of the behavior of the bats and the effectiveness of their visits. In addition, a positive identification of the species of bat involved is often lacking. Many species are still only suspected of possessing flowers which are visited by bats in their native stations (e.g., *Kigelia africana* Benth., and species of *Amphitecna, Parmentiera, Durio, Oroxylon, Caryocar, Tillandsia, Agave, Calliandra, Eugenia, Sonneratia, Barringtonia, Capparis, Crataeva,* and some cacti) (Porsch, 1932; Allen, 1940). This list is based mainly on a morphological study of the flowers of these genera. Porsch (1932) and others have noted that bat-visited flowers (which are night-blooming) are characterized by the emission of a peculiar smell and Jaeger (1954b) lists other morphological features which he believes to be indicative of bat-pollination. There is, however, a distinct lack of careful, sustained observations.

In Ghana, fruit bats are not uncommon and detailed studies of bat-pollination are possible on those species of flowering plants whose floral morphology and behavior are such as to suggest that they will be visited. *Parkia clappertoniana* Keay was the first species chosen for attention and photography was used to make a record of observations on visits.

PARKIA CLAPPERTONIANA

A Likely Subject

Parkia clappertoniana Keay is a tree of medium height (up to 22 meters) which is common in the Guinea Savannah and Sudan Savannah of West Africa, and is distributed eastwards to the Sudan itself.

Dalziel (1937) enumerates the many uses to which this tree is put by Africans. The seeds and the pulp around the seeds are eaten, while an infusion of the bark is used in tanning leather and in coloring earthenware and the mud walls of houses. For these reasons the species is tended rather than eliminated even in those areas of Sudan Savannah where intensive cultivation has destroyed most of the indigenous vegetation.

Flowering takes place in the dry season between the months of November and January, but a spasmodic production of inflorescences can occur during other months. Trees tend to lose and replace their leaves during the period of flowering but defoliation is not always complete and some branches may retain all of their leaves during these months. Flowering is usually confined to branches from which the leaf fall occurs. When it is at an end a vigorous development of new leaves takes place.

The inflorescences (fig. 2B) are spherical in shape, with a diameter of about 5 cms, and contain upwards of 2,000 flowers. They are suspended at the ends of stout but flexible peduncles up to 34 cms long (Keay, 1955) and about one cm in diameter. These are placed on the tree in such a way that the balls of flowers usually hang clear of surrounding foliage. In this respect, the inflorescence of *P. clappertoniana* is similar in emplacement to the single flower of the Baobab (*Adansonia digitata* L.) which Jaeger (1945) showed to be bat-visited. This similarity between *Parkia* and *Adansonia* can also be seen when comparing the globose inflorescence of the former with the ball of stamens in a single flower of the latter. All the flowers of the *Parkia* inflorescence are not fully fertile for there is a cylinder of flowers in the region where the inflorescence is attached to the peduncle in which only the filaments of the stamens are well developed. Occasionally, dehiscent anthers occur here, but the chief function of these flowers appears to be the secretion of nectar at night. This nectar accumulates in a small circular depression (fig. 1). Up to 5 ml of nectar has been recovered from a single inflorescence in one night.

The flowers emit a weak fruity scent but the strong unpleasant odor characteristic of some other bat-visited flowers (e.g., *Adansonia, Kigelia* and *Ceiba*) is absent. The inflorescence exhibits protandry and as the flowers of the spherical portion pass through stages of opening, anthesis, withering of the stamens and, finally, emergence of the stigma, so there is a progressive color change in the inflorescence from red through purple to salmon pink. Anthesis appears to take place an hour or so before dusk and most of the pollen disappears within 12 hours. Although most styles do not elongate until after pollen has been shed, occasional flowers (up to about 24 in an inflorescence) show protruding stigmas at the time of anthesis.

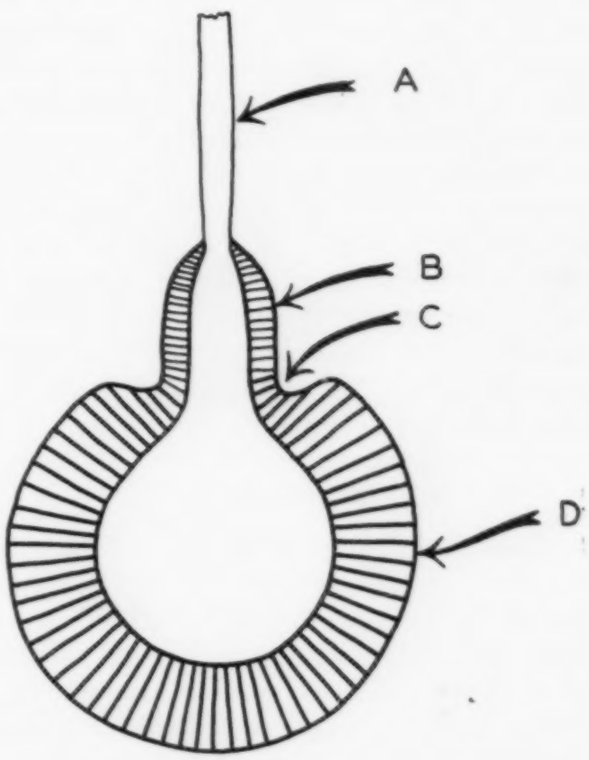


FIG. 1. Diagrammatic section through the inflorescence of *Parkia clappertoniana*. A, stout peduncle; B, sterile nectar-producing flowers; C, ring in which nectar collects; D, potentially fertile flowers.

In the absence of pollination, the flowers fall from an inflorescence, leaving nothing but the bare drumstick-like peduncle. Eventually the peduncle itself, which previously had been capable of bearing a considerable weight, is shed, following the formation of an abcission layer at its attachment to the branch.

All the observations on bats reported in this paper were made on trees of *P. clappertoniana* planted at Achimota (latitude 5° 38′ N, longitude 0° 13′ W). These trees were more accessible than those growing wild in the Guinea Savannah or in the Shai Hills of Ghana where, however, some observations have been made with similar results.

Photographic Methods

The photographic equipment consisted of a Kine Exakta camera with 10.5 cm, 15 cm and 25 cm lenses. Electronic flash equipment was used with the camera focussed on a particular inflorescence. Exposures were made when bats visited the selected inflorescence. The series of photographs used in figures 2–6 was later built up from a selection of many which were taken on different nights.

The flash did not appear to affect the behavior of the bats, neither did the use of electric torches. This is contrary to the experience of van der Pijl (1956) who reported that the *Macroglossus* visiting a *Musa* inflorescence in Indonesia was disturbed by a photographic flash and did not return.

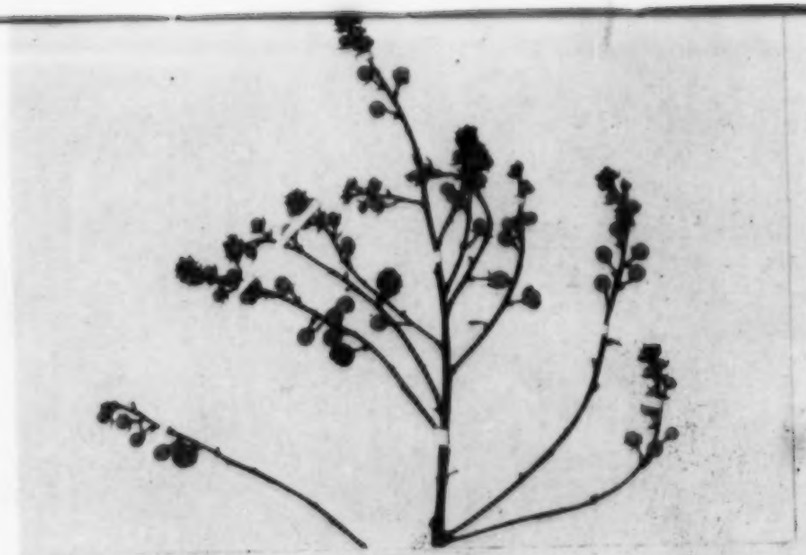
Observations

During the daytime the only visits recorded to inflorescences of *Parkia clappertoniana* were by an unidentified sunbird and a social wasp (a species of *Belanogaster*), each seen on a single occasion. The sunbird moved from one inflorescence to another and appeared to peck at the flowers. The wasp spent 10 minutes or more on a single inflorescence, paying no attention to the flowers but remaining in the depressed ring which had contained nectar the previous night. By contrast, crepuscular and nocturnal visitors were observed regularly.

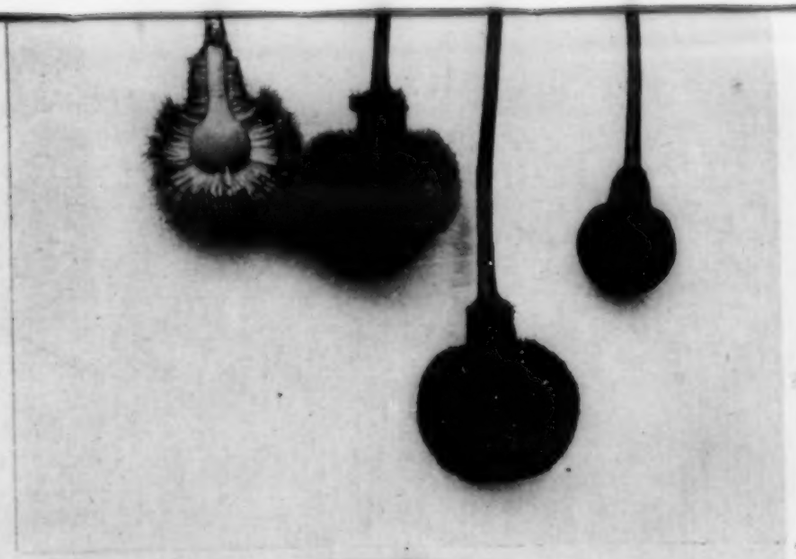
As dusk approached but whilst it was still light (17.30–18.00 hrs. G.M.T.), the inflorescences were visited by such large numbers of bees that a conspicuous droning could be heard several yards from the tree. A similar congregation occurred at dawn. These bees were actively crawling over and flying around the inflorescences, apparently collecting pollen and nectar from the fertile flowers (fig. 2D). They were identified as *Apis mellifica* Linn., the honey bee. On the whole they confined their visits to inflorescences in the staminate state and paid little attention to the nectar in the basal "ring." It is unlikely that they were of any significance as pollinators.

The earliest bats to arrive at the trees were *Epomophorus gambianus* Jentink. This is a medium-sized bat (with a wingspan of about 60 cms) and rather slow-moving. Usually the first individuals arrived just as visibility began to be restricted by the fading of daylight (circa 18.00 hours G.M.T.). The visits of this species tended to last for about 20 minutes each evening (although visits were occasionally made later), and the flight of the bats tended to be restricted to the upper regions of the tree where the inflorescences were least encumbered by neighboring branches. The shortness of the visit and the restriction of flight to the upper part of the tree canopy made this species of bat difficult to photograph. Figure 3A–D shows *Epomophorus gambianus*.

When landing on an inflorescence this bat would grip the ball of flowers with its hind feet. The approach was slow, and after the landing had been accomplished, the bat hung on for as long as 15–45 seconds. It would push its snout into the circular depression on the inflorescence and take up the nectar with a lapping action of the tongue. Apparently in order to keep its balance, it would maintain a slow flapping movement with its wings

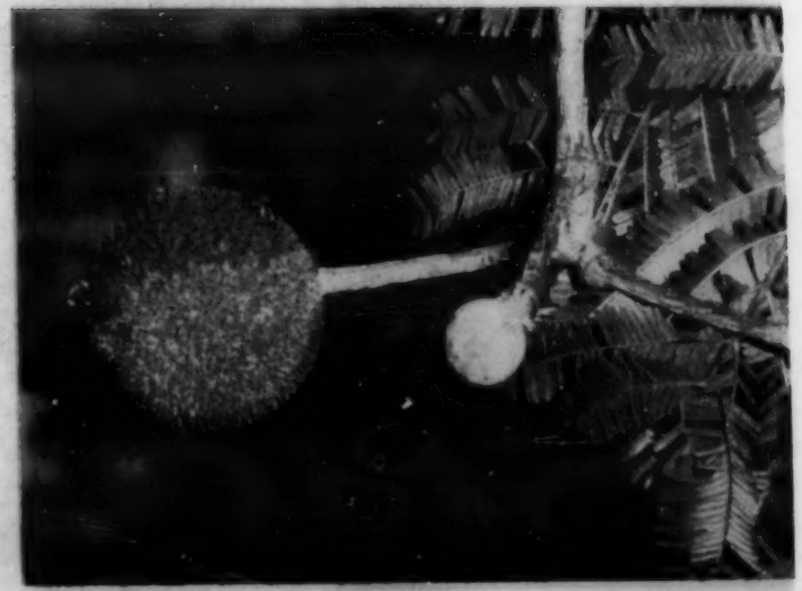


A



B

C



D

FIG. 2A. Inflorescence of *Parkia ulei* (from a herbarium specimen, T. A. W. Davis No. D.122, Simuni Creek, British Guiana).

FIG. 2B. Inflorescences of *Parkia clappertoniana*. Right to left; unopened bud, staminate condition, pistillate condition, section through pistillate inflorescence.

FIG. 2C. Infrutescences of *Parkia clappertoniana;* view from beneath canopy.

FIG. 2D. Bees pollen-collecting from *Parkia clappertoniana* before dusk.

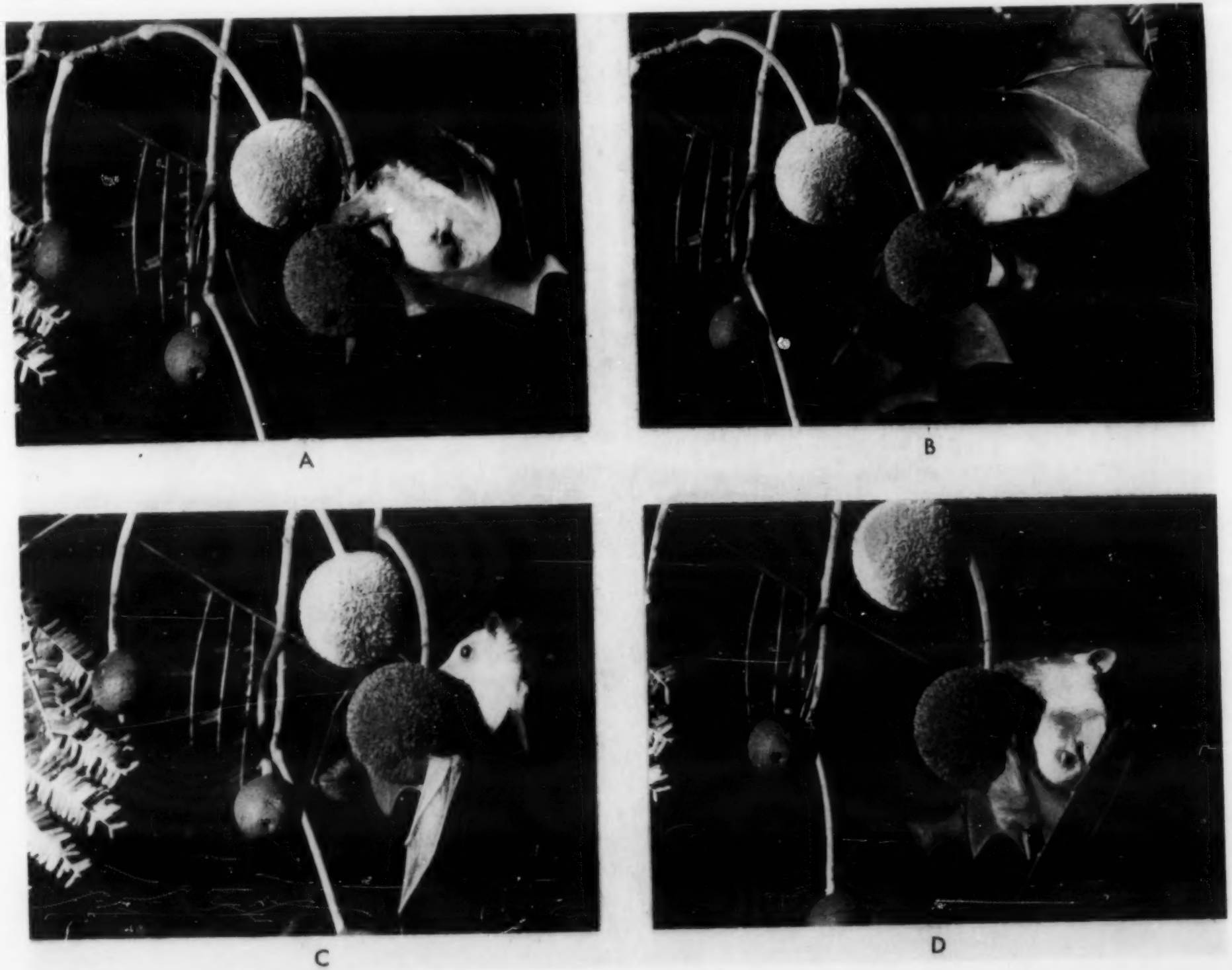
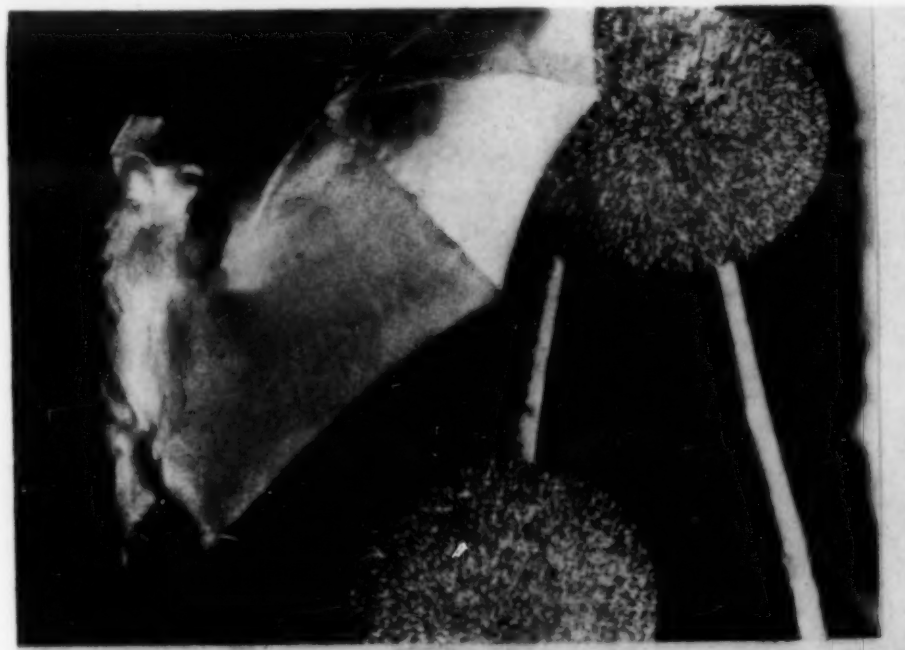


FIG. 3A–D. *Epomophorus gambianus* ♀ visiting and lapping nectar from *Parkia clappertoniana*.
Note grasping with hind legs whilst wings are flapped.



A

B

C

D

FIG. 4A–D. Approach of *Nanonycteris veldkampii* to *Parkia clappertoniana*. Note vertical position of body.

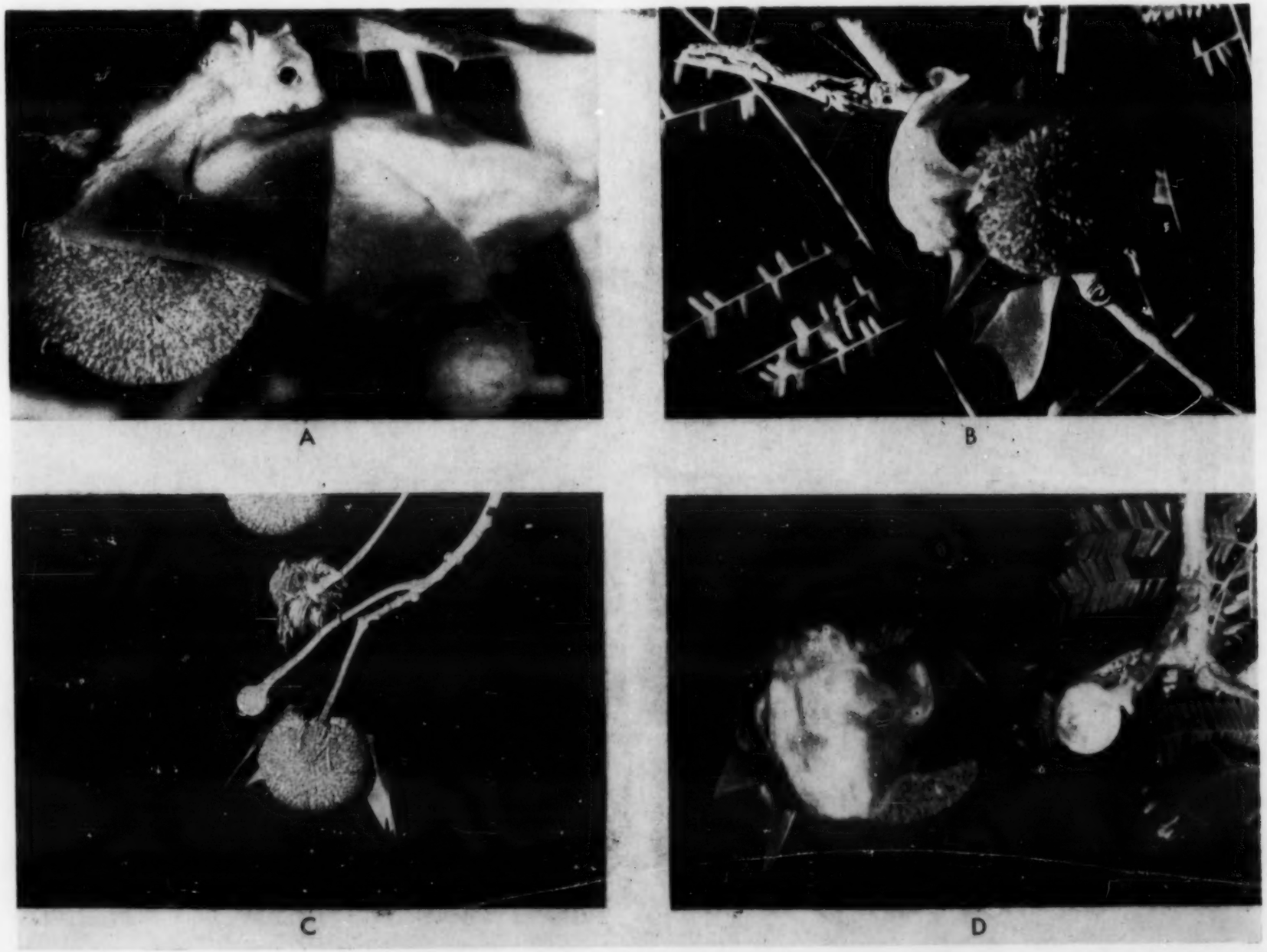
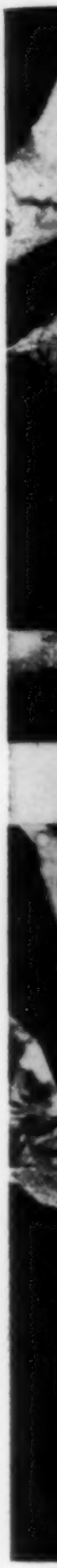


FIG. 5A–D. Landing of *Nanonycteris veldkampii* on *Parkia clappertoniana* followed by nectar-lapping.



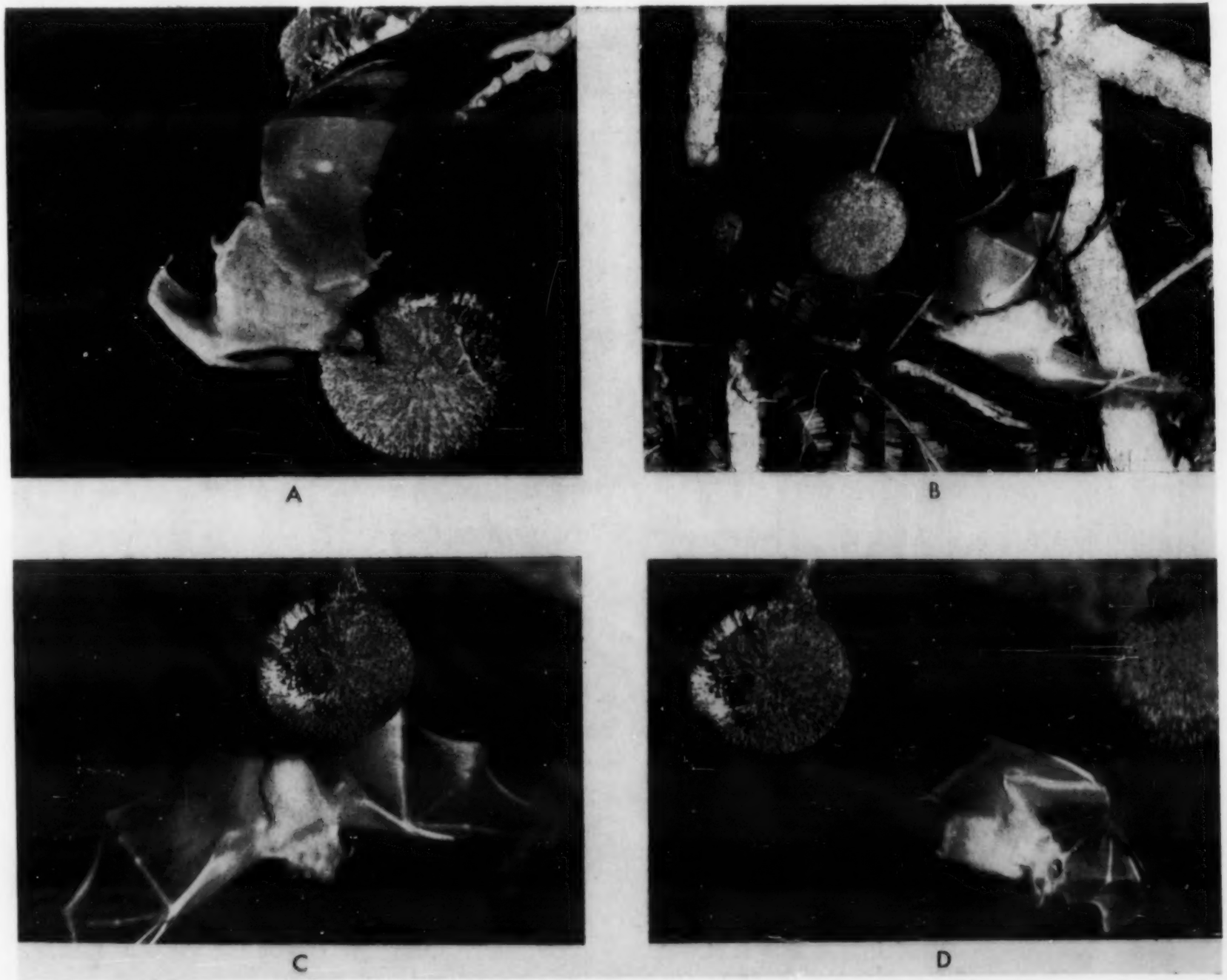


FIG. 6A–D. Departure of *Nanonycteris veldkampii* from *Parkia clappertoniana*. Note bat's narrow tongue still protruding in figure 6D.

(fig. 3B). Less commonly the wings were folded and partly wrapped around the inflorescence (fig. 3C). Both methods of support can result in pollen being transferred from inflorescences in the staminate condition to the body of the bat from which they may be deposited subsequently on an inflorescence with exserted stigmas.

Inflorescences tended to be visited repeatedly, especially when up to a dozen bats were flying around a single tree. There appeared to be no discrimination by the bats between inflorescences in the staminate or pistillate conditions, but immature inflorescences were not visited and neither were those from which unfertilized flowers had begun to fall.

During the daytime these bats (*Epomophorus gambianus*) roosted in tall trees of *Khaya senegalensis* A. Juss. which had been planted about 400 meters away some 20–25 years ago. This species is a savannah tree which is commonly found growing in those parts of Ghana where *Parkia clappertoniana* is indigenous.

As darkness gathered, a second species of bat would make its appearance. This was identified as *Nanonycteris veldkampii* (Jentink) Matschie, a smaller animal with an average wingspan of about 34 cms. This species tended to arrive just before the departure of the *Epomophorus,* about 18.30 hours G.M.T., and visits would be paid to the tree with varying intensity during the night until the early hours. On several occasions it was observed that individuals of *Epomophorus* which were hanging on to inflorescences of *Parkia* were harassed by *Nanonycteris.* This usually resulted in the larger bat releasing its hold and flying away.

Nanonycteris is a quicker and more agile flyer than *Epomophorus* and tended to visit inflorescences all over the tree. The methods of approaching and landing on an inflorescence, of clasping with the wings, and of the subsequent departure are to be seen from the composite sequence of photographs (figs. 4–6). The time spent by a bat of this species on an inflorescence varied from 1–30 seconds but was, on the whole, considerably shorter than the time spent by *Epomophorus* in the same position. From direct observations and from the photographs it is clear that *Nanonycteris veldkampii* clasps the inflorescence with its wings, holding on with its thumbs, and applies its face to the depressed ring containing the nectar. The nectar is then lapped with the narrow, rough tongue. Departure from an inflorescence is rapid and details cannot be observed easily, but from the photographs it would seem that the bat first throws itself backwards. It may then drop below the inflorescence, completing a somersault before opening its wings and flying away (figs. 6B & 6C), or it may do a half-roll (fig. 6D). No evidence was obtained of any flower-eating by the bats, but it was noticed that during their visits to older inflorescences, unfertilized flowers were occasionally knocked off.

Neither species of bat visited the trees before or at dawn. At the time that observations were being made, a flock of the large fruit bat *Eidolon helvum* Kerr visited the neighborhood. They crawled over the flowers of a flowering Silk Cotton Tree (*Ceiba pentandra* Gaertn.) Standing less than 30 meters away from a specimen of *Parkia clappertoniana* which was being actively visited by *Epomophorus* and *Nanonycteris,* but they did not visit the *Parkia* at all.

Specimens of *Epomophorus gambianus* and *Nanonycteris veldkampii* were shot whilst visiting *Parkia* inflorescences. There was abundant pollen on the fur of their breasts and faces, which, after microscopic examination, was easily identified as consisting of the 16- (or 32-) celled polyads of *P. clappertoniana.* Dissection of the stomachs showed that they contained a sticky fluid. This was undoubtedly nectar which had recently been swallowed. There was, however, no sign of pollen in the stomach as had been found, for example, by van der Pijl (1936) in

Eonycteris spelaea shot after visiting *Parkia roxburghii* at Buitenzorg.

Epomophorus gambianus is an African bat distributed from Senegal to Nigeria in the West and across to Abyssinia in the East. *Nanonycteris veldkampii,* however, is only to be found in West Africa, between Liberia and the Cameroons (Rosevear, 1953). Both species belong to the Megachiroptera, the section of the Chiroptera (bats) which is confined to the Old World and which is composed almost entirely of fruit-eaters. The tongues, teeth and stomachs of some of these bats have become adapted to the lapping and digestion of nectar.

Discussion

The observed behavior of the bats *Epomophorus gambianus* and *Nanonycteris valdkampii* on inflorescences of *Parkia clappertoniana* is similar to the description given by Danser (1929) of the visits of unidentified bats to *P. roxburghii* at Buitenzorg, and the subsequent description of visitations by *Eonycteris spelaea* to the same species by Docters van Leeuwen (1938). *Parkia roxburghii,* however, has a somewhat different inflorescence from that of *P. clappertoniana.* In the former the basal flowers are sterile but their staminodes have conspicuously elongated filaments (Danser, 1929) which may possibly offer some protection from rain to the nectar accumulated in the reservoir. Male and bisexual flowers are produced successively towards the apex of the inflorescence. As the inflorescence is pendant, the staminodal flowers lie uppermost. The nectar in *P. roxburghii,* according to van der Pijl (1936), is produced as milky drops which ooze out from the male flowers.

From the brief description given by Danser (1929) it is clear that considerable damage is done to the flowers of *Parkia roxburghii* by visiting bats. Docters van Leeuwen (1938) found their stomachs to be full of pollen, anthers and nectar. Damage to this extent was never observed in *P. clappertoniana.*

The mechanism by which bats are attracted to and locate inflorescences of *Parkia clappertoniana* is not known, but it is interesting that the floral parts of this species lack both the creamy color and the semi-foetid smell which characterize a number of cheiropterophilous plants and which some writers (e.g., Porsch, 1932) have regarded as serving to attract bats when illumniation is poor. Some South American and East Indian *Parkia* species have whitish cream flowers, but, of these, only *P. roxburghii* G. Don is known as yet to be cheiropterophilous.

Alternative foods for bats

The two species of bats found visiting *P. clappertoniana* are also fruit-eaters. In Achimota they may be seen attacking the "fruits" of *Ficus umbellata* Vahl (trees of which grow in the vicinity of the *Parkia* trees) and they probably eat the fruit of other species in addition. They appear to chew the fruits, swallowing the juice and expectorating the solid matter. It seems likely that the nectar of *Parkia* plays only a minor role in the diet of these fruit bats.

The flowering period of *Parkia clappertoniana* in West Africa seldom lasts as long as four or five months in any one year, so that non-migrant bats such as *Nanonycteris* and *Epomophorus* cannot depend entirely on *Parkia* for their food. Indeed, it is apparent that *Parkia* nectar is insufficient in quantity or in its range of constituents to provide the total food supply of an actively growing and reproducing mammal of the size of these bats. Allen (1940) and van der Pijl (1956) have both remarked on the necessity for an alternative source of food for bats which are visiting the flowers of a species with a limited flowering period; this alternative may be provided not only by flowers of another species, however, but by fruits (or even bark as in the case of *Eidolon helvum*) or the bats may migrate. We have not been able to establish a suitable sequence of flowers at Achimota, and here the *Epomophorus* and *Nanonycteris* supplement their floral diet with fruit.

The significance of bat visits

In attempting to assess the significance to the plants of the visits by these bats, one must bear in mind that there may be a balance between the disadvantages of floral destruction and the beneficial aspects of pollen-transfer. Since in *P. clappertoniana* little or no destruction was observed, it can be concluded that the visits of the bats are, at least, not harmful. However, even on trees which are freely visited by bats, most peduncles fall without having borne any fruit and even on those which persist, the number of fruits that finally ripen is small (usually between one and nine at Achimota). On the other hand, a tree which overhangs a road on which traffic was fairly frequent, produced practically no fruit at all. Bat visitors to this tree tended to be very rare indeed (probably due to the disturbance).

Another feature which adds weight to the view that the bats are really active as pollinating agents is illustrated moderately well in figure 4. There is a tendency for the fruits of *Parkia clappertoniana* to be formed on one side of the inflorescence only—the side which faces the periphery of the tree canopy. This is the usual direction by which bats approach, for they usually fly around the tree and then move in to land on an inflorescence.

It is not yet known whether *P. clappertoniana* shows true self-incompatibility but experiments are in progress to determine this, and will be reported elsewhere. It may be significant that recent work with *Acacia decurrens* Willd. by Philp and Sherry (1946) and with *A. mollissima* Willd. by Moffett (1956) has demonstrated self-incompatibility for the first time in the Mimosaceae. In both species there was a reduction in seed-setting to 30% when out-crossing was prevented. If self-incompatibility does occur in *Parkia clappertoniana*, the value of the strong-flying bats as pollinating agents could be very great where more or less isolated trees occur. However, where this species occurs naturally, trees are sometimes in much closer proximity and, in these circumstances, pollen-transfer might take place by other vectors. In any case, the strong protandry makes a necessity of pollen-transfer from inflorescences in the staminate condition to those which are pistillate, for even those anthers which are still attached when the styles elongate have shed their pollen. The large pollen masses (polyads c. 85 μ in diameter, containing up to 32 individual grains) are too heavy to be carried any significant distance by wind although geitonogamy following the rubbing together of adjacent inflorescences is not impossible. It is, however, unlikely as adjacent inflorescences are rarely in the appropriate conditions.

Geographical and historical relation between bats and the genus *Parkia*

The genus *Parkia* has a disjunct pantropical distribution with its species clustered in three main areas, viz. Africa (largely in the West); South America (largely in Amazonia) and the West Indies; and continental south-east Asia and the East Indies. In two of these areas the inflorescences are known to be visited by bats which appear to play an effective part in pollination. These bats (*Eonycteris spelaea* and *Cynopteris brachiotis* visiting *P. roxburghii* in the East Indies and *Epomophorus gambianus* and *Nanonycteris veldkampii* visiting *P. clappertoniana* in West Africa) all belong to the family Pteropidae (Megachiroptera). The inflorescences of the *Parkia* species which they visit appear, in many ways, ideally suited to pollination by their agency. Thus, the inflorescence hangs clear of the foliage on a flexible but stout peduncle. It produces a large reservoir of nectar at night in a position where it can be taken by large flying animals which, at the same time, receive or transfer pollen which adheres to the fur of their adpressed breasts.

Similar inflorescences are to be found in some of the species of the genus which occur in South America, for example *P.*

nitida Miq. or *P. pendula* Benth. Nothing, however, is known of any visitors to these New World species where members of the Megachiroptera cannot be the agents of pollination (for they are entirely Old World in distribution). It is greatly to be desired that observations will be made in the forests of tropical South America to discover the nature of the pollen-vectors for these species.

The oldest known fossil remains which can be definitely identified as bats appear to be those found in Eocene (including 'Paleocene') beds in North America (Scott, 1937) and Germany (Revilloid, 1922). The German remains are of well differentiated members of the Microchiroptera, not unlike living members of that sub-order. Megachiropteran fossils appear in Oligocene beds in Italy. The existence of such highly evolved bat-like creatures in the early to middle Tertiary period suggests that the Chiroptera as an order may have been differentiated at an earlier date but there is, as far as we know, no record of such forms. Bats, like birds, appear to be under-represented in fossil beds even when they seem likely to have formed a significant element of the fauna (Simpson, 1937).

The only definite records of New World bats visiting flowers are those referred to on pages 449 and 450. The two bats mentioned there (*Anoura geoffroyi* (Peters) Grey and *Glossophaga soricina* Pall.) are members of the family Phyllostomidae in the sub-order Microchiroptera (Miller, 1907). The Phyllostomidae is an entirely New World family which includes a majority of insectivorous species. However, all the fruit-eating bats of the New World belong to this family and Allen (1940) believes on morphological grounds that these frugivorous types have evolved from the insectivorous stock. This suggestion receives support from the relative numbers of species in each feeding group.

The further suggestion has been made that the fruit-eaters of the New World represent a more recent evolutionary development than the Old World Megachiroptera (in which all species, with the possible exception of some species of the genus *Nyctimene,* are fruit-eating).

Recently (Koopman & Williams, 1951; Williams, 1952), accounts have been published of fossil bats from a Jamaican cave. It is not stated that any of the fossils found had been of fruit-eaters, but it is interesting to note that members of the genus *Glossophaga* (which is known to include a flower-visiting species) were found only in the most recent remains, in the surface and subsurface layers.

Parkia, being a pan-tropical genus of forest and savannah trees with several species in each geographical region, can be assumed to have achieved its wide distribution at a remote period. There is reason to believe that this may have preceded the Eocene with its first fossil record of bats. Whether this distribution of the genus *Parkia* occurred at the latitude of the present tropics as a result of Continental Drift or by migration through what are now temperate latitudes at a time when tropical climates extended much farther towards the Arctic, it is clear that the Eocene stage is the very latest at which this could have occurred.

According to most statments of the theory of Continental Drift, the separation of the present day continents from the primaeval Pangaea began in the Mesozoic era but as late as the Eocene stage there persisted a slight connection between South America and West Africa (cf. Wulff, 1943).

On the other hand, even assuming the permanent occupation by the continents of their present positions, surveys of Eocene floras such as that by Krystofovich (1929) show that at the warmest time in the Tertiary period only the climate of the southern end of western Europe was tropical or sub-tropical and that, from then onwards in the Northern Hemisphere, there was a continuous decrease in clemency of the climates of all areas, culminating in the onset of the Pleistocene glaciations (cf. Godwin, 1956). Equally,

it is only before the Eocene stage that there could have been contact between tropical floras through Beringia (cf. Cain, 1944). By contrast with *Parkia*, the absence of Megachiroptera from the New World suggests that their evolution came too late for them to be included in a New World fauna, in agreement with their short fossil record. In this connection it should be noted, however, that whereas fruit-bats are tropical in distribution (only rarely reaching into the sub-tropics), insectivorous bats range from the tropics to cool temperate zones. Thus it may be no coincidence that the primitive stock of bats in the New World seems likely to have been insectivorous.

The question then arises as to the nature of the pollen-vectors of *Parkia* at a time when fruit-bats were probably not available. Should the widespread *Parkia clappertoniana* type of inflorescences be considered an example of purely fortuitous pre-adaptation? It seems almost certain, for the New World at least, that the development of fruit-eating and nectar-lapping bats took place subsequently to the origin of the *Parkia* inflorescence-type which we have been considering.

The distribution of variability in *Parkia*

A study of dried material of *Parkia* deposited in the herbarium at Kew revealed that there are some 19 morphologically very diverse species recorded from tropical South America and the West Indies. South-east Asia has yielded 11 species with some conspicuous vegetative variation whereas only 5 morphologically rather similar species are known in the whole of Africa. The ascription of *P. biglobosa* Benth. to the New World as well as Africa (Bentham, 1875; Hutchinson and Dalziel, 1928) appears to be an error and this species appears to occur only in Guinea Savannah regions of West Africa. It might be considered that the difference in species numbers for these three regions could be related to the amount of taxonomic work that has been done in the regions or the frequency of collecting in each of them. The Kew herbarium, however, contains more material of *Parkia* from Africa than from any other part of the world and there is good reason to believe that, comparatively speaking, the West African flora is particularly well known.

An attempt was made to classify the known species for inflorescence-position (upright, spreading or pendant peduncles); presence or absence of a marked staminodal fringe at the base of the inflorescence; inflorescence-shape (monoglobose or biglobose); inflorescence-color (white, yellow or red) and leaflet-size (fine, medium or large). The information used was obtained from herbarium specimens and published descriptions but there were some instances in which neither of these sources was fully informative. The result of this analysis is given in table 1.

It is quite evident that variation is greatest amongst the South American *Parkia* species and is very limited in the African species for the characters chosen. In addition, the characters themselves show a high degree of assortment in the South American species. South-East Asian species are intermediate in the amount of their variation.

In addition to the tabulated characters, there is also a contrast to be seen in the pods which are relatively uniform in shape in West Africa, rather variable in South-East Asia and of strikingly different shapes and sizes in the South American species.

Although there are dangers in the assumption that the region in which a genus shows the greatest amount of variation, in this case South America, is its center of origin, it is at least unlikely that the continent in which the fewest species with the least diversity occur (i.e., Africa) will prove to be the cradle of that genus.

In relation to this suggestion of a New World origin for the genus it may be significant that the inflorescences of such South American species as *Parkia ulei* (Harms.) Kuhlm. and *P. parviceps* Ducke resemble quite closely those of the

TABLE 1. *Characters of* Parkia *species in the Old and New World*

	Peduncle	Staminodal fringe	Inflorescence mono- or bi-globose	Inflorescence color	Leaflet size
South America and West Indies	4 upright	9 with	8 mono-globose	10 red or reddish	11 medium
	2 spreading	10 without	12 bi-globose	7 white	9 fine
	12 pendant	1 unknown			
	2 unknown			3 unknown	
S.E. Asia	10 pendant	2 with	9 bi-globose	8 yellow or yellow-white	2 large
	1 unknown	3 without	2 unknown	3 unknown	2 fine
		6 unknown			7 medium
Africa	5 pendant	4 without	5 bi-globose	5 red	4 medium
		1 with			1 fine

related genus *Leucaena*.[1] In these species of *Parkia*, the inflorescences (fig. 2A) are small (about 1 cm in diameter) and erect and sometimes arranged in racemose groups, quite different from the solitary pendant heads of *P. clappertoniana*. It is most unlikely that species such as *P. ulei* are pollinated by bats but it would be very interesting to know what does visit them. In the appearance and distribution of their inflorescences they may well illustrate the basic type from which the bat-visited types have evolved. According to Wodehouse (1935), North American members of the Mimosaceae are probably insect-pollinated although wind may sometimes play a part.

The evolutionary problem of the inflorescences in *Parkia*

If this interpretation of the evolutionary history of the genus *Parkia* is correct, we are left with an enigma. An inflorescence-type eminently suitable for the attraction of bats and their utilization in effective cross-pollination appears to have evolved in what is now South America from types which are adapted to visits from other pollinators. Yet we must assume that this took place in the absence of bats and that it was only upon arrival in the Old World that the fortuitously adapted inflorescence-type could be made use of by the Megachiroptera. The utilization of Parkias with this type of inflorescence by bats in the Americas, if it takes place, would be a relatively recent development.

Almost inevitably this raises the doubt that, despite the deductions which seem to be most reasonably made from the systematic, geographical and palaeontological data, we are putting the cart before the horse. Either the history of nectar-lapping bats goes back farther than the Eocene (and there were nectar-lappers which are now extinct in South America) or else the genus *Parkia* had its origin in the Old World rather than the New (and the diversity of forms in South America is to be attributed to radiative evolution in a new environment). After all, Croizat (1952), in his highly theoretical treatise on plant geography, has claimed that many families of flowering plants with a similar disjunct tropical distribution entered the New World via the "West African Gateway."

This difficulty of deciding which came first, the presence of bats eager for nectar,

[1] In Index Kewensis (7th suppl., 1929) it is suggested that *P. ulei* should be transferred to the genus *Leucaena* but, apart from any other features, the pollen masses of *P. ulei* and *P. parviceps*, which contain up to 16 small grains each, resemble those of other members of the genus and are utterly different from the large, tricolporate, prolate monads of, for example, *Leucaena glauca* Benth.

or of flowers and inflorescences adapted to their visits is not restricted to the genus *Parkia*. All the evidence from taxonomy, morphology, cytology and phytogeography agrees in demonstrating the great antiquity of the family Bombacaceae (cf. Corner, 1949; Stebbins, 1951; Croizat, 1952; Baker, unpub.), yet this family contains at least two genera (*Adansonia* and *Ceiba*) in which there is a flower-type apparently well adapted to bat-pollination (which has also been observed to occur). This must have been evolved earlier than the Eocene.

The present investigation has served to bring this evolutionary problem to light. Before it can be solved it will be necessary to make careful observations upon the pollination-systems of *Parkia* species in all parts of the tropics where they occur, and not least in South America. Cytological studies may also be useful. Any new palaeozoological evidence which will help to date the origin of the nectar-lapping bats will be of great value and so would be the (unfortunately unlikely) discovery of fossil *Parkia* material. This subject is being opened, not closed.

Summary

A historical survey is made of bats as pollinators. Although a considerable, scattered literature exists, there is a paucity of systematic and sustained observations. *Parkia clappertoniana* (Mimosaceae) has many of the attributes of a cheiropterophilous plant and was chosen for visual and photographic observations in Ghana.

Daytime visitors to this tree at Achimota are not important but near dusk (and dawn) large numbers of bees (*Apis mellifica*) visit staminate inflorescences. At dusk, the bat *Epomophorus gambianus* visits inflorescences in both staminate and pistillate conditions for the abundant nectar which they produce. Later, another bat, *Nanonycteris veldkampii* takes over. The approach, landing, nectar-lapping and departure of these bats is described. Both bats appear to be important pollen-vectors. *Parkia* nectar, however, constitutes only a small part of their diet.

The fossil record of the Chiroptera is not known to reach back beyond the Eocene and the vegetarian Megachiroptera appear to have evolved too late to be able to enter the New World tropics (where nectar-lapping bats appear to have evolved relatively recently from an insectivorous Microchiropteran stock). The genus *Parkia,* however, with a pan-tropical distribution, is likely to be older than this, yet inflorescences of the *P. clappertoniana* type (which appear ideally suited for bat-pollination) occur throughout the range of the genus. This raises the problem of the nature of its pollinators before fruit-bats were available.

Morphological variability in *Parkia* decreases in order from South America through S.E. Asia to Africa. Some South American species are most unlikely to be bat-pollinated and may show a more primitive type of inflorescence, but observations of pollinators here are badly needed. More evidence of various kinds must be collected before the center of origin of the genus and the historical relationship between the development of a suitable inflorescence and the evolution of nectar-lapping bats can be discerned.

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GENETIC STUDIES OF A LABORATORY POPULATION OF *PARAMECIUM AURELIA*, VARIETY 1

R. F. KIMBALL, NENITA GAITHER, AND STELLA WILSON

Biology Division, Oak Ridge National Laboratory,[1] *Oak Ridge, Tennessee*

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INTRODUCTION

Paramecium aurelia has not been used for laboratory studies of population genetics although there are a number of features that ought to make it favorable for this purpose. Some information is available about natural populations, and a number of the questions that are basic to an understanding of the population genetics of this organism have been discussed by Beale (1954), Sonneborn (1955, in press), and Pringle (1956). A population of *P. aurelia* normally consists of animals belonging to a series of different clones that have originated at various times through one of the two sexual processes, conjugation or autogamy. Conjugation allows cross-fertilization between clones, as well as mating within, whereas autogamy is a form of self-fertilization within a single individual and produces complete homozygosis for all loci (see Beale, 1954). Thus a basic question for any population study with this species is the relative frequency of these two types of clones. If most clones in a population have arisen at conjugation, the population should resemble those of other crossbreeding organisms; if most clones have arisen at autogamy, the population will approach the clonal structure characteristic of asexual organisms, though with the special feature that new mutations are made homozygous at the next autogamy after they have occurred. Sonneborn (in press) has discussed these matters in some detail and has given reasons for believing that natural populations of this species are more likely to approach the clonal than the crossbreeding type. He emphasizes that this conclusion is more strictly true for certain non-intermating varieties such as 4 than for others such as 1. Pringle (1956) has found heterozygous clones in nature with a small but appreciable frequency for variety 1; and, since heterozygotes can only be produced by conjugation, this means that conjugation occurs with an appreciable, though perhaps low, frequency in nature.

The purpose of the present work was to see whether an essentially crossbreeding population of variety 1 could be maintained in the laboratory under conditions that are reasonably favorable for conjugation. The results show that this can be done.

METHODS AND RESULTS

Since there is, as far as we know, no direct information on the genetic structure of laboratory populations of *Paramecium aurelia,* it seems worth while to record some observations on such a population, despite their incompleteness. Beale (1954), Sonneborn (1955), and Pringle (1956) have given brief discussions of the basic problems involved, and Sonneborn (in press) has discussed the problems in some detail. There are two types of breeding, (1) conjugation, which allows outbreeding and (2) autogamy, which produces complete homozygosity. Panmixia should predominate if the former is the main process, but a nearly clonal structure should exist if the latter is the main one. The data to be presented show that conjugation predominates in a particular laboratory population of variety 1 of *P. aurelia.*

On April 12, 1955 a test tube population was started from several hybrid clones from a cross of the variety 1 stocks, 90 and

[1] Operated by Union Carbide Nuclear Company for the U. S. Atomic Energy Commission.

CD. The population was grown at approximately one fission per day by mixing the contents, discarding half, and refilling with baked lettuce culture medium daily. A single tube was maintained in this way at 27° C from April until late August 1955 and was then subdivided into four tubes, two at 27° C and two at 31° C. These replicate populations have shown no marked differences and are not separately reported.

The stocks of origin differ from each other in 5 loci (Kimball and Gaither, 1955). Stock CD is homozygous for the recessive alleles clear (*cl*), dumpy (*dp*), and single mating type (mt^{I}) and for the antigen alleles d^{60} and g^{60}; otherwise it is nearly isogenic with stock 90. The latter is homozygous for the dominant alleles of *cl, dp,* and *mt* and for the serotype alleles d^{90} and g^{90}. Only *cl, dp,* and *d* were followed in the population. Depending on the conditions of growth, especially the temperature, a given animal may belong to one of the D serotypes determined by the alleles of *d* or some other serotype determined by alleles at some other locus, such as *g* (Beale, 1954). In the present work, the few isolates that were not of the D type were converted to it by growth in mass culture at 31° C. Heterozygotes for the *d* alleles react with both anti-60D and anti-90D serum; homozygotes, with only one.

At irregular intervals, the tube contents were thoroughly mixed, a sample was withdrawn, and individual paramecia were isolated and allowed to multiply. The cultures that resulted were checked for serotype and the clear and dumpy characters. For some samples, daily isolation lines were established from each isolate, autogamy was induced, and the frequency of normally multiplying exautogamous clones ascertained. The data on serotype and postautogamous growth are summarized in table 1.

The two alleles of the *d* locus have remained in the population in nearly their original equal frequencies. The *cl* allele was rare in the first sample and apparently has been completely lost. The *dp* allele was present at nearly the original 50% frequency in the first sample, was greatly reduced by the second, but apparently is still present in a low, though undetermined, frequency in the most recent samples.

The frequency of the three serotypes has probably been fairly constant since August 1955. The marked deviation of the third sample from the others and from random mating expectation suggests that false positive reactions with anti-60D serum caused some of the 90D isolates to be misclassified as heterozygotes. Tests for false reactions were made with some of the other samples, and none were found; nevertheless, this is the most reasonable explanation of the deviation.

The relative frequency of animals belonging to exconjugant and exautogamous

TABLE 1. *Samples of laboratory populations of* Paramecium aurelia

Date of sample	Number in sample	Percentage failing to survive to test	Percentage frequency of serotypes among the isolates that survived*			Percentage frequency of inviable and poorly growing cultures after autogamy
			6	6/9	9	
May 23, 1955	163	2.45	37.74	33.96	28.30	20.4
August 12, 1955	180	3.33	23.56	44.83	31.61	62.1
December 5, 1956	360	10.83	23.36	62.93	13.70	—
December 31, 1956	224	13.84	32.12	47.67	20.21	—
January 3, 1957	90	18.89	27.40	42.47	30.14	85.3
January 6, 1957	240	17.50	30.30	43.94	25.76	—

* 6, reacted with only anti-60D serum; 6/9, reacted with both antisera; 9, reacted with only anti-90D serum.

clones can be derived from the frequency of the heterozygous as compared to the homozygous serotoypes. Heterozygotes can only arise at conjugation; and, if it is assumed that mating and survival are random in respect to serotype, the frequency of animals belonging to exconjugant clones can be calculated from the second, fourth, fifth, and sixth samples in table 1 to be about 90%. The excess of homozygotes over random expectation can be attributed to about 10% of animals from exautogamous clones. The actual frequency of autogamy among all sexual events in the population is undoubtedly higher since, as will be shown below, exautogamous clones are considerably less likely to survive than exconjugant ones. The data simply show that of all animals present at any one moment, about 90% belong to exconjugant clones and 10% to exautogamous ones.

The average interval between successive sexual events, conjugation or autogamy, must be rather long because the frequency of animals with fragments of the old macronucleus is low. At either event, the macronucleus fragments into a number of pieces which remain visible for several fissions before eventually disappearing. On several different days in January 1957, samples from the tubes were examined for the presence of macronuclear fragments, and the frequency was found to be nearly constant at 11%. Since fragments persist for several fissions and the average fission rate was about one per day, the frequency of sexual events must have been considerably less than 11% per day. Clones cannot persist indefinitely without a sexual event because of the well-known aging phenomenon; consequently there can be no lines of descent that do not eventually undergo such an event or die, and the average interval between successive events must be appreciably greater than 10, quite possibly 20, 30, or even more days.

During the year and a half, there has been a large accumulation of what are, apparently, deleterious mutations. This is shown in table 1 by the increase in frequency of isolates that failed to grow sufficiently to be tested for serotype and by the great increase in poor growth and inviability after autogamy. Further information on this poor growth and inviability was obtained by two observations made in January 1957. A group of 90 conjugant pairs was isolated from the tubes; 49.4% grew poorly or died. There was a high correlation between the two members of a pair (85.6% alike), as would be expected if death and poor growth had a nuclear basis. The still greater frequency of death and poor growth after autogamy (table 1) suggests that an appreciable part of the mutations were recessive. A few days after the group of conjugants was obtained, a group of 360 single animals was isolated from the tubes, and only 23.3% grew poorly or died. Thus at least some of the genotypes that were unfavorable in isolation were also unfavorable in the tube; otherwise the frequency of poor clones should have been more nearly the same in the conjugant and single-animal isolations.

In conclusion, random outbreeding through conjugation is the predominant sexual process in these populations, but it should be emphasized that the conditions were especially favorable for conjugation. The mt^I allele, if still present in the population, would help keep the ratio of the two mating types more nearly equal than would be expected if only its wild-type allele were present. The daily limited feeding, which brings the paramecia into condition for conjugation each day, and the dense population also favor conjugation. Sonneborn (in press) has pointed out that variety 1 is better equipped as an outbreeder than some of the other varieties of *P. aurelia*. It is unlikely that conditions in the wild would be nearly so favorable for conjugation; the mt^I allele has been found in only one collection source, and wild populations are rarely if ever so dense as laboratory ones. Nevertheless, Pringle (1956) has found some

hybrid clones in nature; therefore it is certain that conjugation does occur.

The great accumulation of deleterious mutations was unexpected and certainly does not represent the condition of all *Paramecium* mass cultures. This accumulation is probably the consequence of the random outbreeding population structure, which allows the accumulation of recessive lethals and of chromosomes that are favorable in certain combinations and not others. Conditions that favor autogamy would be expected to retard or prevent the accumulation of so many unfavorable types.

Discussion

The major conclusion from this work is that it is possible in *Paramecium aurelia* to establish a laboratory population consisting mainly of exconjugant clones and therefore comparable to populations of other crossbreeding organisms. Several factors have favored this outcome. Variety 1 has a relatively long interval after either fertilization process during which conjugation but not autogamy will recur. The method of daily feeding brings the animals into the proper physiological state for conjugation once a day while keeping the fission rate low and the immature period, before autogamy can recur, long. A further favorable feature may have been the introduction of the mt^{I} allele into the population from stock CD. Animals homozygous for this allele are always mating type I whereas animals with the wild-type allele may be either type I or type II but are more often the latter at the temperatures used. The mt^{I} allele, especially if it were present in the right frequency, would tend to equalize the frequency of the mating types and so maximize the probability of animals of opposite mating type meeting each other and conjugating.

A less expected result of the work was the high frequency of inviable and slowly growing clones that arose after conjugation and autogamy. It seems probable that this was a consequence of the crossbreeding population structure. In our previous experience with variety 1, it has not been uncommon to find appreciable death among the exautogamous descendants of individuals isolated at random from stock cultures; but the frequency of death has rarely if ever been as high as in the present case. The conditions in stock cultures, which are fed at somewhat irregular and relatively long intervals, are probably considerably less favorable for conjugation than those in the present populations. Further support comes from our experience that animals isolated from stock cultures of variety 4 only rarely give rise to poorly growing or inviable exautogamous progeny, and Sonneborn (in press) has pointed out that variety 4 is more strictly an inbreeder than variety 1.

An outbreeding population structure would be expected to allow recessive lethals to accumulate to a higher frequency than a clonal one. It is not certain, however, that this is the only factor involved. The high frequency of inviable clones after conjugation suggests a high degree of allelism among lethals and could be taken to mean that a few (3 or 4) lethal and deleterious mutations reached quite high frequencies because of favorable selection in the heterozygous state. There are a number of uncertainties, however, in converting the frequency of poorly growing clones to the number of loci involved, especially when this frequency is as high as it is after autogamy; consequently it would be unwise to place much reliance on this last conclusion.

Summary

It was shown that it is possible to maintain a population of *Paramecium aurelia* in the laboratory under such conditions that a large portion of the animals belong to exconjugant rather than exautogamous clones. Under these conditions, the population should resemble in its behavior populations of crossbreeding organisms rather than clonally reproducing, asexual organisms. During the course of the year and a half that the population was main-

tained, recessive lethal and deleterious mutations accumulated to such an extent that most homozygous segregants produced by autogamy were inviable. The basis for this accumulation is briefly discussed.

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EVOLUTIONARY RELATIONSHIP BETWEEN ENTOMOPHILOUS PLANTS AND ANTHOPHILOUS INSECTS [1]

E. E. Leppik [2]

The Hormel Institute of the University of Minnesota, Austin, Minnesota

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Most students of floral ecology and insect behavior agree today that bees and flowers are closely and mutually interrelated in evolution as reciprocal selective factors (Frisch, 1950, 1954; Grant, 1949; Schneirla, 1951; Butler, 1954, p. 6). But neither the evolution of flower types to their present perfection of colors and symmetry, nor the sensory development of insect pollinators, which might have caused the gradual floral differentiation, are yet satisfactorily explained. So far, no attempt has been made to present theories or speculations on how the flowering plants, which form the main part of the vegetation on earth, have come to be as we see them today. Almost all recent writers hold the view that the evolution of the flowering plants is still as great a mystery as ever (Just, 1952; Good, 1956; Thomas, 1956). It is urgently important, therefore, to explore the expected parallelism between the development of flowers and of insects, and to establish its evolutionary significance.

In some earlier papers (Leppik, 1948a, 1956), an attempt was made to arrange some directly observable tendencies and trends in floral differentiation into a historical sequence, which would mirror, according to the present theory, the main trend of the accelerated evolution of entomophilous angiosperms. A new idea, to be discussed in this article, concerns a conjectural sensory mechanism which governs the tropheclectic behavior of anthophilous insects, and coordinates their selective activity among fast-evolving flower types. Recent investigations suggest that this conjectural mechanism (or mechanisms) has been established in insects step by step during their sensory evolution, and is functioning now as the principal determining factor for floral differentiation (Leppik, 1956, 1957a).

Ability of Pollinating Insects to Distinguish Flower Types

The long-lasting debate among biologists as to whether colors or scents attract pollinators has finally been resolved by experimental findings which indicate that bees have both a keen sense of color and a sharp perception of odor. In addition, the color sense of insects has been found to be supplemented by an accurate perception of form and symmetry (Frisch, 1914; Hertz, 1929; Leppik, 1953b, 1954; Kugler, 1955, p. 104–107).

There is further evidence and considerable experimental proof that at least hymenopterous pollinators are able to distinguish third dimensions and forms of bilateral symmetry. In this respect the bumblebees have been more fully studied,

[1] Much of the material used in this report was collected by the writer while working at the Tropical Research Institute of the University of El Salvador in Central America during the years 1953 and 1954. Dr. Aristides Palacios, Director General, and Dr. Adolf Meyer-Abich, Constituent Member of this Institute, helped the author to solve many technical problems during this study.

Dr. Th. Just, Chief Curator of the Chicago Natural History Museum, helped the author in discussing many problems of this study. Miss Karen M. Heyerdahl, Principal Secretary of the Hormel Institute, assisted in the preparation of the manuscript.

[2] Present address: Iowa State College, Department of Botany and Plant Pathology, Plant Introduction Station, Ames, Iowa.

and are known to possess a keen visual perception of form and depth (Kugler, 1942, 1943, 1955; Werth, 1949, 1956). These insects have also a special liking for stereomorphic and zygomorphic forms of so-called "bumblebee flowers," which plants have almost the same geographical distribution as bumblebees. The ability of insect pollinators to distinguish form and symmetry is further mirrored in their steadfastness to definite flower types, as described below.

A further remarkable capability of some groups of pollinators to recognize and remember numeral patterns in flowers is discussed elsewhere (Leppik, 1948a, 1953b, 1954, 1955c, 1957b). There are at least thirteen basic combinations of numbers that certain groups of pollinators can recognize and remember as definite symmetrical patterns: many, few, single, five radial, five bilateral, four radial, four bilateral, three, two, six, eight, ten, and twelve. In nature, insects encounter these "figure numerals" regularly as tri-, bi-, tetra-, penta-, hexa- and polymerous types among pleomorphic [3] and stereomorphic flowers. Being conditioned to these basic numeral patterns and remembering their size, color, and frequently also odor, a "literate," let us say, pollinator can easily distinguish his nectar plants from hundreds of flower types displayed to him in a landscape and in a foraging area. The ability of insects to distinguish the above-described numeral patterns is evidenced so far by experiments, special tests, and field observations in honeybees, stingless wild bees (Melaponidae) and several tropical butterflies (Leppik, 1954, 1956).

It should be noted here that in this sequence of "figure numerals," numbers 7, 9, and 13 are absent. Obviously, such combinations, which cannot be arranged symmetrically so that they could be easily distinguished visually without counting, are not perceptible to insects. Plants, obedient to their insect "breeders" only very infrequently hold such "nude" numbers in their flowers. Consequently, the numeral system of insects, in spite of its broad applicability to hundreds of combinations, differs basically from all known numeral systems of man (Leppik, 1956).

The fact that certain plant species, or even varieties, are discernible to pollinating insects has been known at least since Aristotle (see transl. 1910) and is repeatedly confirmed by appropriate experiments (see Grant, 1950b; Bateman, 1951; Leppik, 1951, 1954, 1955a; Werth, 1956; and others). But we cannot expect from insects such taxonomic knowledge in the anthropomorphic sense, as is sometimes erroneously indicated. Mather (1947) has good reason to argue that there is a range of similarity between forms at and below the specific levels, over which discrimination by the bees is absent or imperfectly developed.

Actually, insects are neither capable of identifying plant species as taxonomic units in our sense, nor of discriminating interspecific and intervarietal groups of plants. Our taxonomic classification and species identification is based upon the phylogenetic relationships among plants, which are unknown to insects. But anthophilous insects do recognize their food plants as definite "flower types," no matter whether these types embrace species, genera, varieties, or other taxonomic units. In nature, these types most abundantly coincide with definite species, less frequently with varieties or genera, leading observers sometimes to the erroneous idea that insects are capable of interspecific and intervarietal discrimination of plants. Floral ecologists have often shown that when two or more distinct species bearing the same type of flower are planted on

[3] *Amorphic* flowers are primitive clusters of discolored leaves, without particular form. *Haplomorphic* types are semispherical forms like Magnolia and Water-lily. *Actinomorphic* types have radiate symmetry. *Pleomorphic* type class includes bi-, tri-, tetra-, penta-, hexa-, octo- and oligomorphic forms, with distinctive figure numerals in flowers. *Stereomorphic* flowers have three-dimensional structure and *zygomorphic* flowers have bilateral symmetry (Leppik, 1956, p. 256).

the same bed, pollinators will intermingle these species.

From all these facts and arguments, it can be concluded that a flower is recognized by insects as a whole, which means more than a mere sum of all characteristics such as color, form, number of flower parts, size, and odor. In experiments, however, honeybees, wild bees, and wasps learn quickly to locate sugar syrup according to a single characteristic, such as color or odor. In nature, on the contrary, pollinators rarely encounter such simple combinations of floral characteristics. Flowers are not just formless colored or odorous spots on green vegetation, but rather, represent the finest combinations of colors, form, and symmetry. Nonetheless, every single flower type, if considered as a whole, is clearly distinguishable even from a considerable distance. It is reasonable to assume, therefore, that from a distant view, a flower group appears as a colored patch that helps the pollinators to locate a foraging area. Upon reaching the area, the pollinators stay close enough to distinguish one flower type from another. Bees decide quickly which flower to choose, and then inspect each flower very closely, possibly to determine odor, nectar guides, and other special characteristics. Butterflies, on the contrary, spend considerable time in the air before descending to some single flower.

The Role of Pollinating Insects in the Evolution of Flower Types

Much new information has accumulated during the past decades on the selective ability and activity of pollinating insects among flower types. In this brief review, however, no effort is made at complete coverage of literature in question (see Koelreuter, 1761; Darwin, 1862; Mueller, 1876; Loew, 1884; Lovell, 1918; Small, 1919; Kugler, 1942, 1943, 1955; Werth, 1956, Hodges, 1952, 1955). Nor can the genetic approach to the problem, as promoted by Stebbins (1950), Grant (1949, 1950, 1952), Mather (1947, 1951), Bateman (1947, 1951), Straw (1955, 1956), and others, be discussed at length. Main emphasis will be placed on the evaluation of the newest research records on the evolutionary corelation between insects and flowers, as described elsewhere (Leppik, 1955a, 1956, 1957a, b).

Recent investigations suggest that two types of selection are performed by insects among flowers. First they choose the most promising and structurally accessible flower type for their permanent visits. Dancing honeybees recruit other fellow workers to their previously selected plant species and soon the whole bee colony is steadfast[4] to the same flower type in a foraging area. Bees, bumblebees, and other specialized, mentally more developed pollinators ordinarily prefer plants of higher evolutionary levels, like legume plants and composites, and turn to lower flowering plants mainly in the case of food scarcity. Having once made their choice, steadfast pollinators remain long faithful to a single flower species, favoring a particular *ethological isolation* (Grant, 1949, 1950a, b) of certain types from one another. Such intraspecific selection and subsequent isolation must be an obvious advantage for the seed production and rapid expansion of certain selected species.

A second type of selection is performed by pollinating insects among varieties and ecotypes of the same species, provided that some varieties have distinguishable characteristics and particular value for selecting insects. Insofar as a pollinator is capable of distinguishing some varieties, it tends to select the best food plants from the available material. This selection is

[4] *Steadfast pollinators* are conditioned to visit the same flower type at a given time, evidently after their previous choice. *Constant pollinators* are involuntarily bound to a single, a few, or many plant species during their lifetime. E. Loew calls them, respectively, monotropic, oligotropic, or polytropic visitors. According to this viewpoint, honeybees are polytropic because they are not bound with any special nectar plant. But they exhibit, nevertheless, a high rate of steadfastness to their previously chosen flower types, and so do many other pollinators (Leppik, 1953b, p. 230, footnote; 1956, p. 234).

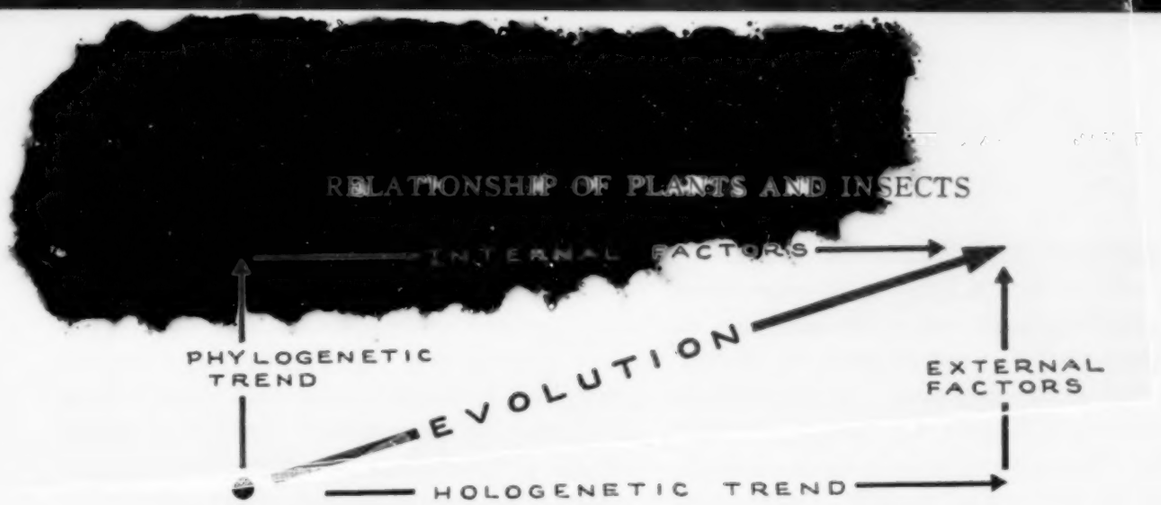

FIG. 1. Presumptive interaction of internal and external factors on the course of evolution, as exemplified in the differentiation of flower types under the selective activity of pollinating insects.

consequently directed instinctively by insects toward the improvement of plant material in an area and refinement of the biochemical composition of selected plant groups, as described elsewhere (Leppik, 1955a, p. 49). Carrying pollen from one plant variety to another, insects unconsciously produce new combinations of genes and new idiotypes. But they can "consciously" select some of these new types for their continuous visits and further crossings as soon as these new types attract the attention of pollinators as better food plants.

In their permanent search for better sources of food, insects become unconscious carriers of pollen and important plant "breeders." Guided by inborn instincts, their many-sided selective activity is directed through numerous generations towards the same goal of getting better nectar plants, which are marked at the same time with more precise combinations of colors and symmetry. The same inherited instincts drive myriads of individuals of the same species into a well coordinated selective work resulting in the development of special flower types, as described below.

Even if an insect does not "breed" or "choose" in the anthropomorphic sense of the word, their instinctive activity nevertheless results in a continuous "selection" among their food plants. On the level of innate reactivity to the visual stimuli, a definite flower may release in an insect more, or more complete, responses than others, which condition may cause insects to "select" one definite flower type for their continuous visits. Besides, a flower visitor can always learn that some flowers are provided with better nectar deposits and are more easily accessible than others. The steadfastness and the constancy [4] of pollinators are, therefore, most natural consequences of their selective ability and activity.

Consequently, the most vital processes in the development of entomophilous plants, such as fertilization, seed production, and the selection of descendants, are controlled by insects, and the evolution of these plants is considerably influenced by the sensory behaviour of their pollinators. Insects pollination is therefore a very special type of *natural selection,* exercised by insects in search of better food plants. But it can be equally considered as a particular type of *"sexual selection"* whereby pollen collected from definite plants is transferred to the selected individuals of the same species for subsequent fertilization. In another paper this special type of selection is defined as "tropheclexis," i.e., search of food connected with selection of better types of food plants (Leppik, 1955a, p. 49).

In addition, many other regulating factors of biotic, physical, and genetic nature affect the general trend of evolution as a biotic whole or "holon." All these factors may be treated jointly under two groups: internal or phylogenetic (inheritance, new gene combinations, new idiotypes) and external or hologenetic [5] fac-

[5] *Hologeny* is defined as a genesis and historical development of the biotic whole or holon (Leppik, 1948a, b, 1953a, p. 67).

tors (physical and biotic environment, natural and sexual selection, tropheclexis, etc.). Both groups act independently of each other and are attempting to convey the evolution of organisms into different directions, which may be sketched as in figure 1. The evolution is therefore merely a result of these two trends, each composed of many factors, as defined and described in another paper (Leppik, 1955a). The present view is in accord with the morphological treatment of the flower as presented by C. L. Wilson and Just (1939) and the typological approach as summarized by Th. Just (1939, 1952).

Basic Flower Types and Their Evolutionary Trends

A comparative study of contemporaneous flower types reveals that there is a restricted number of more generalized basic forms and a great many of specialized flowers than can be derived from basic forms. Basic types are represented exclusively in phylogenetically older plant groups, whereas the derivatives are found mostly in the specialized flowers of higher evolutionary levels.

According to their form and symmetry, six morphologically graded series or *"type classes"* can be established among flowers, as follows: amorphic [3] → haplomorphic → actinomorphic → pleomorphic → stereomorphic → zygomorphic. This method of typological classification appears natural and corresponds to the main evolutionary sequence of flower types (see below).

For instance, one needs only to take a sunflower head apart to see that a zygomorphic ray floret is really a remolded stereomorphic tubulate flower, the later one being formed from an actinomorphic pentamerous type, which for its part has evolved obviously from a haplomorphic prototype (Small, 1919). In the buttercup family (Ranunculaceae), this evolutionary sequence is clearly expressed in the floral structure of the ecologically highly specialized Superranunculae (Leppik, 1948b). A dissection of highly zygomorphic flowers of *Aconitum* and *Delphinium* reveals the successive evolution step by step from a stereomorphic (such as *Aquilegia*), pleomorphic, actinomorphic, haplomorphic, and finally from an amorphic prototype. In the pseudanthium of *Dichromena ciliata,* an entomophilous beakrush from the tropics, are demonstrated successive evolutionary trends from amorphic → haplomorphic → actinomorphic, and so on (Leppik, 1955b).

Still further evidence supporting the above projected evolutionary sequence of flower types can be obtained from the obvious parallelism between the evolution of flowers and sensory development of certain insect pollinators, as described below.

In a previous paper an attempt was made to arrange existing flower types according to their assumed historical development from more primitive and generalized structures to the very specialized flowers of higher angiosperms (Leppik, 1948a). It appeared appropriate to subdivide the whole historical sequence of flower types into five or six successive periods, as described below. There is a good deal of conclusive evidence that during every one of these periods, a definite *evolutionary level* has been attained in the floral development, in which a corresponding morphological *"type class"* achieved its final form and shape. Once established and fixed genetically in some phylogenetical group or groups, a "type class" has obviously remained long without considerable change in its principal characteristics, but has split and specialized into smaller typological units. As a matter of fact, all above mentioned "type classes" are still represented in the contemporaneous flowers, some of them having preserved their ancient characteristics, and others becoming rather modern and specialized.

Later on this scale of floral differentiation has been used for testing sensory capabilities of different groups of insect pollinators in various geographical areas and climatical zones. A striking correlation

has been established in this study between the graded series of floral differentiation and increasing sensory abilities of pollinators to distinguish the above mentioned and below described "type classes" of flowers. The six observable levels in floral differentiation correspond to six determinable stages in the sensory development of insects, as sketched roughly in figure 3, and described in another report (Leppik, 1957).

After some terminological corrections and a few changes in its structure, the above-mentioned preliminary schema of floral differentiation is presented here in more proper form for further criticism and for possible practical application by students of evolution. It became necessary to separate numerate flower types from a very expansive radiate level and to join accordingly all types with a definite number of semaphylls [6] (petals, sepals, ray flowers, etc.) into a separate type class of pleomorphic flowers. This type class corresponds to the numerate stage in the sensory development of certain insect pollinators, being characterized by the determinable ability grade of these insects to distinguish figure numerals (Leppik, 1956).

In figure 2, the six evolutionary levels are marked from the bottom to the top with Roman numbers I–VI. Main progressive trends are indicated by arrows pointing upward. Arabic numbers indicate parallel trends in various phylogentic plant groups such as Monocotyledones, Tubiflorae, Campanulaeae, Compositae, and Ranales.

(I). The *primitive level* at which *amorphic* flowers do not yet possess any special symmetry or particular colors. A primitive flower consists of an unrestricted number of stamens and pistils, sometimes surrounded by a number of bracts or discolored upper leaves. It does not need any special sensory abilities of pollinators to distinguish such primitive flowers from common leaves of plants. Primitive flowers cannot offer much sweetness to their visitors, and they are commonly exploited by unskilled pollinators. Although this primitive type is not very common among recent plants, it is obvious that first entomophilous angiosperms must necessarily have possessed flowers with such similar primitive characteristics. Such primitive types appear also when a wind-pollinated plant secondarily becomes entomophilous (see *Dichromena, Salix, Mimosa,* and other examples, Leppik, 1955b).

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(II). The *simple level* with an *haplomorphic* arrangement of petals, if any, and simple colors like yellow, white, or greenish. These flowers are visited mainly by beetles and flies, whose mental abilities do not reach much higher from their *simple stage* of development. *Magnolia, Liriodendron, Nelumbo, Nymphaea* and other phylogenetically primitive genera of the order *Ranales* have flowers of such simple level.

(III). The *third radiate level* is characterized by an *actinomorphic* or *radiate* symmetry. Flower parts are arranged in one level with stamens, pistils and nectar deposits. Flowers of this level frequently have pure colors, like white, yellow, blue, red, and so on. There is substantial evidence that these flower types evolved during a time when the main groups of pollinators reached the *third stage* of their sensory development, which includes the ability to distinguish colors other than green, white, and yellow, and patterns of radiate symmetry.

[6] *Trophosemeions* (τροφός = food, σημα, σημείον = mark, sign) or *"food marks"* are colored petals, upper leaves, bracts, etc., which help pollinators to locate food plants. They are composed of *"semaphylls,"* in contrast to *sporophylls* —the stamens and pistils of ordinary flowers. Trophosemeions are different from "nectar guides," which are special pointers of nectar deposits inside of flowers (Leppik, 1956, p. 236–240).

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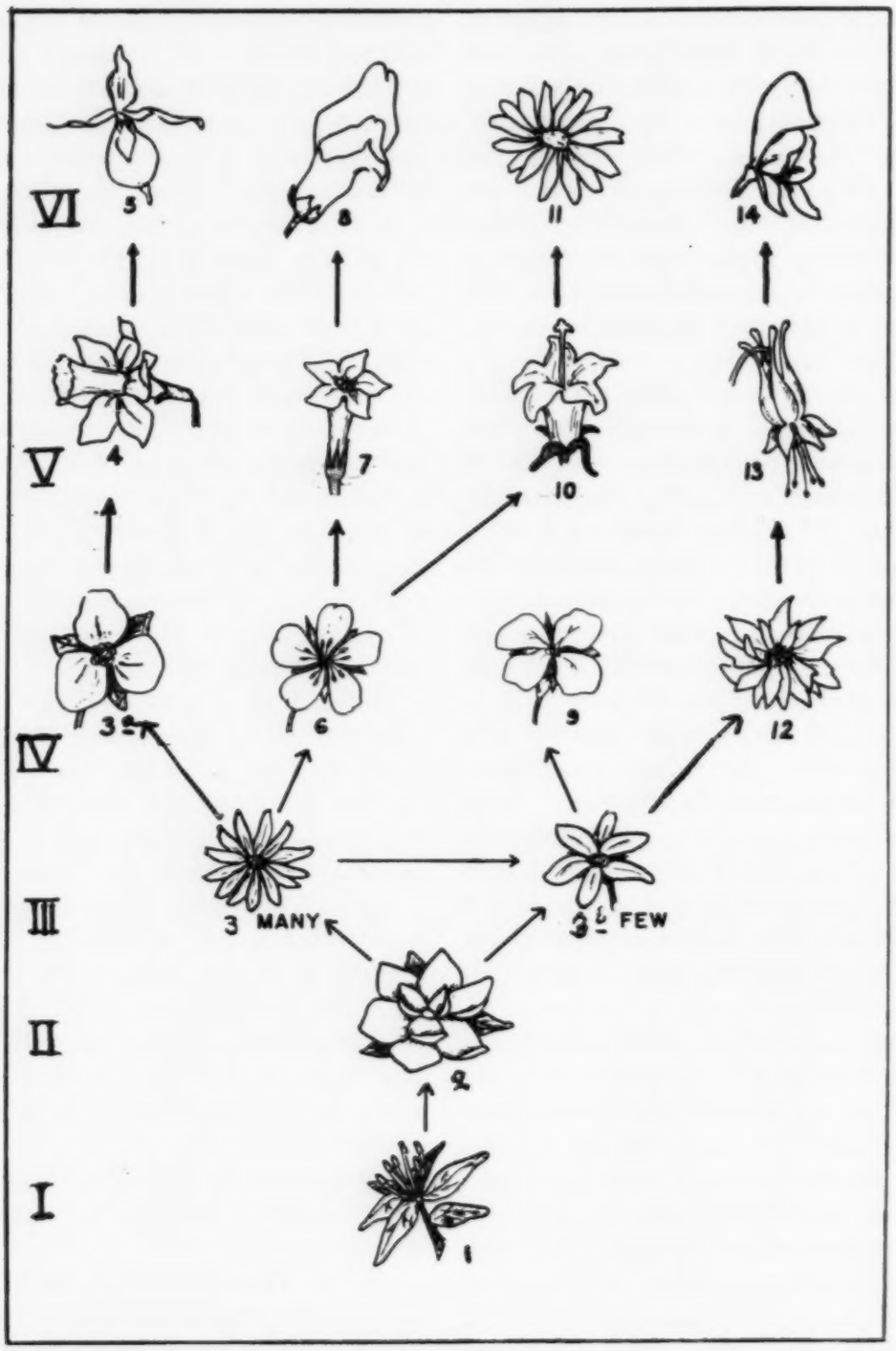

FIG. 2. Observable trends in the evolution of flower types. I level: amorphic types ("paleomorphic" according to R. B. Gordon, see in text); II level: haplomorphic types; III level: actinomorphic types; IV level: pleomorphic types; V level: stereomorphic types; VI level: zygomorphic types of bilateral symmetry. Assumable phylogenetic trends are indicated by Arabic numerals: $1 \rightarrow 2 \rightarrow 3 \rightarrow 4$ etc. (Rearranged scheme from a former paper: Leppik, 1955a.)

(IV). The *numerate* level is characterized by the appearance of distinctive figure numerals in flower types. Former radiate flowers begin to reduce the number of petals and fix them to 3, 4, 5, 6, 8, 10 etc. In some former sketches, numeroid types have been included in the radiate level, but it seems more natural

to segregate them into a separate level, and pleomorphic type class.

(V). The fifth *"protected" level* of the evolution of flower types includes *stereomorphic* flowers with protected nectar deposits. This structure requires in their pollinators an ability to distinguish three-dimensional patterns in order to locate the nectar in the depth of the flower. Colors, symmetry, and "figure numerals" are similar to the IV level.

(VI). The *highest* level in the floral development contains many special types of zygomorphic flowers. All these very specialized types have in common their bilateral symmetry, variegated but harmonious combinations of colors, and the finest odors. According to present knowledge, this superior level of flowers corresponds to the highest stage in insects, that of recognizing bilateral symmetry.

This evolutionary sequence, however, is in agreement with the recent view about the phylogenetic development of angiosperms. It is generally believed that apetalous groups are derived from petaliferous ones, that numerous floral parts of each kind are more primitive than few parts, that apopetaly is more primitive than sympetaly, that hypogyny is more primitive than perigyny or epigyny, that separate and distinct parts of all kinds are more primitive than either adnation or connation, and that each of these changes has taken place independently in several groups (Bessey, 1915; Hutchinson, 1926; Cronquist, 1951, p. 15).

The Phenomena of Convergency and Recapitulation in Floral Evolution

In the above-outlined standard scheme of floral evolution, only basic flower types of six subsequent levels are described and pictured in figure 2. Such evolutionary sequence is especially well represented in Ranunculaceae, including haplomorphic (*Paeonia*), actinomorphic (*Anemone, Ranunculus*), pleomorphic (numerous species), stereomorphic (*Aquilegia*) and zygomorphic (*Aconitum*) types of five subsequent levels in a single family (Leppik, 1948b). An analogous broad hologenetic amplitude can be observed also in Liliiflorae, an order which includes representatives of four type classes. All other orders and families of angiosperms are restricted to one or two type classes, and only seldom reach the third class (Leppik, 1955a, fig. 5).

Beside the two main trends in the floral evolution of Dicotyledoneae and Monocotyledoneae, there are many cases of *convergency* and parallel developments, where analogous flower types have been evolved in various phylogenetically unre-

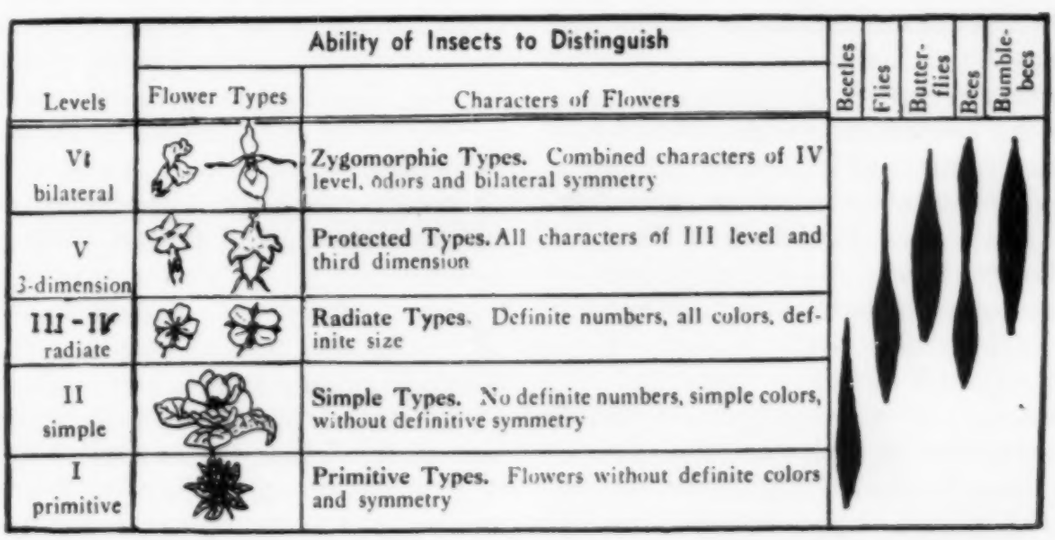

Fig. 3. Relative ability ranges (black) of various groups of anthophilous insects to distinguish flower types of definite evolutionary levels (I–VI).

lated plant groups. Particularly rich in such examples are radiate and protected evolutionary levels, including numerous actinomorphic, pleomorphic, and stereomorphic types of striking similarity in most various plant groups. In most cases of convergency, some common pollinator, or at least insects with similar instincts or of the same stage of sensory development, might be suspected to have played a role in "selecting" and "breeding" analogous types in unrelated plant groups.

Following are some examples of a convergent evolution among flower types.

Dichromena ciliata Vahl represents an entomophilous trend among wind pollinated Cyperaceae. This white beak-rush has an established relation with tropical insects and developed secondarily a showy white "pseudanthium," formed by involucrated upper leaves. The effect of this imitated "flower" is striking, and the plant is frequently visited by stingless wild bees (Meliponidae), bumblebees, and honeybees (Leppik, 1955a, b).

Among the varieties of *Dichromena ciliata* are less developed haplomorphic types, others with well established radiate symmetry, and some which bear constantly five white leaves in their involucres. The development from haplomorphic to actinomorphic and from polyphyllous to pentaphyllous structures is well demonstrated, which tendency corresponds to the general trend of floral evolution, as pictured in figure 2.

Lantana camara L. is a tropical member of the Verbenaceae with a remarkable tendency to arrange its flowers into a radiate inflorescence, imitating an actinomorphic type of a single flower. The central flowers differ from the peripheral ones by color, the latter being arranged in some varieties like petals (Leppik, 1954, p. 158, photo 3, right).

Numerous further progressive trends are exemplified in specialized flower types which are pollinated by some definite group of insects. These trends occur frequently among stereomorphic and zygomorphic flowers, and are correlated with the sensory development of their pollinators. Well known examples are so-called bumblebee flowers, which are bilaterally symmetrical, such as *Aconitum, Delphinium, Aquilegia, Iris,* and *Antirrhinum.*

Some North American species of the normally pleomorphic genus *Rhododendron,* which are pollinated here by bumblebees, tend to develop slightly zygomorphic flowers, marked with a yellow "bumblebee spot" on the upper petals.

Another remarkable phenomenon in the evolution of flower types is a *recapitulation* of the above described main historical sequence of floral differentiation in some phylogentically restricted plant groups. Frequently the entire evolutionary sequence of the angiosperms (amorphic → haplomorphic → actinomorphic → pleomorphic → stereomorphic → zygomorphic), which occurred during several geologic eras, is repeated in a new form over a relatively short period of time, such as represented in the capitulum of the Compositae, cyathium of the Euphorbiaceae, etc.

Various regressive and rudimentary organs, such as deformed upper leaves, bracts, involucres, functionless staminodia, sterile outer flowers in an inflorescence, and sometimes even ordinary leaves may initiate a new evolutionary departure. From this scanty material, most colorful structures are formed, step by step, such as the showy upper portion of *Poinsettia,* and prominent white bracts of *Cornus florida.* Further examples are: attractive pseudanthium of *Dichromena ciliata,* variously colored synanthia (heads) of Compositae, petal-like staminodia of *Canna* and brightly colored flowering shoots of *Bougainvillaea.* Whatever the origin of these new structures, in their final stage of development they all exhibit a striking resemblance to a true flower. Moreover, these secondarily developed imaginary flowers fulfill now the ecological function of true flowers, attracting by their form and color the attention of insect pollinators.

A detailed analysis of these flower-like

structures reveals their evolutionary trend from the amorphic arrangement of initial leaves or bracts to the haplomorphic and actinomorphic types, with an observable tendency toward pleomorphism, stereomorphism, and zygomorphism. Furthermore, a noticeable parallelism exists between the evolution of these imaginary flowers and the phylogenetic sequence of their bearers (Leppik, 1955a). In this case, it would be extremely difficult to explain how some plant leaves, bracts, or stamens recapitulate hurriedly the whole course of floral evolution and become showy parts of a flower. But by taking into consideration the sensory capabilities and innate behavior patterns of insect pollinators, the whole course of floral evolution appears simple and natural.

According to the present theory an accelerated evolutionary development among flower types may take place when a plant group is exposed to insect pollinators whose sensory development has reached a higher stage than the corresponding evolutionary level of the flowers (see above). In this case pollinators instinctively select ecotypes and possible mutants from the available material, whose color, form or size seems to them closer to the types to which they are innately conditioned. Real differences in these flowers in the beginning may be very small but nevertheless perceptible to the insect eye, such as variations in color, form, size, symmetry, and odor. When these morphological differences are accompanied by a noticeably better nectar or pollen supply, or are more easily accessible to certain pollinators, the latter may remain steadfast to these varieties for a long time. An intensive crossing and mixing of pollen among definite varieties produces an abnormal number of new idiotypes, which are displayed to the pollinators for further selection. From such polymorphic material it is possible for certain pollinators to select definite types they prefer for one reason or another.

Among entomophilous plants there are numerous concrete examples for such progressive floral evolution and some few cases of a retrogressive trend, as pointed out above and described elsewhere (Leppik, 1954, 1955a, b, 1956). Degeneration of petals and semaphylls is a common consequence of a secondarily introduced anemophily among flowering plants. Exchange of specialized pollinators to some mentally less developed groups of insects results in an observable regression in floral structure. Zygomorphic types may revert to stereomorphic and actinomorphic to haplomorphic, and so on. Such examples occur quite frequently among Compositae, Ranunculaceae, Euphorbiaceae, and in many other families.

A Conjectural Sensory Mechanism of Antophilous Insects

In all probability there are definite series of inborn instincts and inherited reflexes in anthophilous insects, which function automatically as responses to the visual stimuli produced by certain flower types. Some reactions in these insects seem to be acquired as a result of experience "learning," and could be classified as conditioned reflexes. Obviously such conditioned reflexes, produced by some visual stimulus repeatedly over a long period of time, become finally established in the nervous system of insects as inherited reflexes. Many reflexes are known to be interrelated, so that a reaction to a certain stimulus may act as a stimulus for a second reflex, this for a third one, and so on until the full series of definite actions is completed. In many other cases complicated sensory processes occur for which no explanation is proposed. But every process which occurs even once must have a mechanism, whether we understand it or not (Huxley, 1942, p. 509).

Though the specific sensory mechanisms are not yet established experimentally, the existence of such a clockwork in anthophilous insects is nevertheless well evidenced by the particular behavior and instinctive activity of this group of insects. Thus it is possible to advance, with con-

siderable accuracy, a reliable explanation of the functions of this mechanism, as described below. In this paper we want to define such mechanism as a combination of certain sensory processes which result in a definitely co-ordinated physical activity of insects. We tend to call this sensory mechanism "conjectural" in order to stress its specific presumptive nature and to distinguish it from the general mechanistic concept, such as "a mechanism of a clock" (see the definition of "mechanism" in Webster's Intern. Dictionary).

A classic example of such stereotypic series of instinctive activities of anthophilous insects can be seen in the behavior of the Pronuba moth, as described already by Aristotle and quoted now in most text books of general biology. Pollination of many other entomophilous plants is an equally complicated process, which requires a high degree of innate capabilities, and existence of a regulating sensory mechanism in their pollinators.

Some very specialized pollinators take no food from flowers, but are guided by their mating instincts, which in some insects are unusually strong and complex. A well known example is the *pseudocopulation* between certain wasps and orchids. Several species of *Ophrys* and *Cryptostylis* are visited and pollinated by male wasps for the striking resemblance of these flowers to female insects. During mating, male insects fly from flower to flower, being attracted mostly by varieties and possible mutants among orchirds with certain resemblance to female insects, which are not yet born at that time. Not finding true females, deceived males finally pseudocopulate with some flowers, pollinating unconsciously these orchids with heterogenous pollen. No wonder, therefore, that in such unusual circumstances the evolution of the above-mentioned orchids is turned toward strange insectiferous forms, such as represented by *Ophrys insectifera* L. This strange phenomenon was first described by Pouyanne (1916) from North Africa, by Coleman (1928) from Australia, by Wolf (1950) and Kullenberg (1952) from Europe (see also Ames, 1937).

Existence of a further sensory mechanism, which tends to direct the evolution of flower types in a predetermined direction, has been ascertained recently in honeybees, bumblebees, stingless wild bees, tropical butterflies, and seems to be inherent in many other insect groups. Though the mechanism itself is not yet fully explained, its existence and functioning are well demonstrated by the particular behavior of these insects. It is further evidenced by the actual trends of floral evolution, which can be traced back through several geological eras (Leppik, 1953b, 1955a, 1956). This mechanism has evolved gradually in pollinating insects, apparently parallel with the differentiation of flower types. In its lower stages, this mechanism is functioning analogically in many insect groups, but becomes more specialized in the higher stages of its development. In higher, specialized pollinators it consists now of six successive stages which can be determined as six ability grades of these insects to distinguish six main type classes and a number of specialized forms of flowers, as described above. In mentally less evolved insect groups, this mechanism is simpler, consisting only of some lower grades of the sequence.

This classificatory mechanism must of necessity consist of a definite series of sensory processes which are similar in many insect groups whose food searching activity is restricted mainly to flowers. In the early beginning this mechanism could have been fixed as a response to a primitive visual stimulus, produced by an amorphic aggregation of yellow stamens on a green or whitish background of upper leaves, which reflex has guided these pollinators to the ancient paleomorphic flowers. It is obvious that some varieties or ecotypes among those primitive flowers with more intensive colors and more regular symmetry must have produced a stronger stimulus and released more complete reflexes in insects than

other flowers. Such variations must have challenged primitive pollinators to a continuous selection of "better" types among flowers, in particular when the coloration and symmetry has concurred with a higher nectar or sugar content of those flowers. A gradual differentiation of the next haplomorphic type class must have resulted from such a selection, and several new reflexes added to the sensory mechanism of those primitive pollinators. Still additional stimuli were needed to awaken a sense for two-dimensional symmetry in insects, which was necessary for the recognition of the third, actinomorphic type class of radiate flowers. New combinations of form, symmetry, and colors in flowers must have stimulated insects for further progressive development. Step by step, responses to figure numerals, third dimension, and finally to bilateral symmetry must have been added as successive stages for the development of the sensory mechanism in anthophilous insects. This main trend of the sensory evolution of insects is reflected in the floral differentiation from the amorphic to haplomorphic, actinomorphic, pleomorphic, stereomorphic, and zygomorphic type classes, as pictured in figure 2.

Under the existing conditions, this evolutionary sequence is probably the only possible course of development for both insects and plants. Such a mutual evolution of insects and plants makes both participants highly interdependent. Except for some retrogressive trends, there seems to be only one logical way for the progressive expansion of simple reflexes into more complicated sensory processes enabling the insect to distinguish two-dimensional flower types, numeroid, three-dimensional and finally the forms of bilateral symmetry. The floral differentiation from the elementary amorphic material to the haplomorphic, actinomorphic, pleomorphic, stereomorphic, and finally to the zygomorphic types, seems equally natural. Such successive development of flower types is also in accord with the progressive genetical variability of flowering plants, such as production of new mutants resembling the next higher (or lower) type class. The genuineness of this evolutionary sequence is evidenced further by its parallel occurrence in numerous genetically unrelated plant and insect groups.

Once established and fixed genetically, these sensory mechanisms must function continuously through centuries, governing the behavior of anthophilous insects. Every additionally adapted process must necessarily increase the corresponding capability grade of insects to distinguish flowers of the next higher type class. Consequently the less evolved insects must be attracted ordinarily by lower, and the more evolved by higher type classes, which is of course in accord with well established facts. Such stereotyped behavior of anthophilous insects is obviously an important regulating mechanism, which tends to direct the selective activity of pollinators and subsequently the evolution of flower types in a definite predetermined trend.

Field observations have shown that pollinators commonly are most attracted by the flowers of highest possible type class accessible to them, and that they select such classes from the available material for their permanent visits. Once steadfast on a certain type, they tend to pick up varieties and ecotypes which are closer to the next higher type class (Leppik, 1954, 1957b, 1956.) These insects seem to perceive instinctively that a higher "rank" of flowers, according to "nomenclature" of their own, means a better source of food, which perception is of course in accord with the biochemical evolution of flowering plants.

In these circumstances the above described evolutionary sequence must necessarily be valid also in the development of the present-day flower types. Recent investigations show that this supposition is not only well-grounded in its general trend, but is also convincingly evidenced in numerous special cases. Recapitulation of this sequence is well demonstrated

in the differentiation of flower heads of the Compositae (see above), of secondary flowers of the Euphorbiaceae, of pseudanthium of the *Dichromena ciliata* (Leppik, 1955b), and in many other cases.

It is convincingly evident that insects cannot remember an unrestricted number of flower types, or even as many as are displayed to them in a local flora at a time. Actually they need to know only a series of three or four out of six basic patterns, which represent six main type classes of flowers. These basic patterns are repeated again and again in different size and color in numerous plant groups. Frequently symmetrically similar flower types are marked by figure numerals or by distinctive odors. For that reason various local floras, in spite of their different taxonomic composition, exhibit an unexpected resemblance in their basic types, even in such distant areas as the arctic and tropics on the Eurasian, American, and African continents. In their specialized types these floras show, of course, a greater variability. Several comparative studies of the writer in these areas have shown a proper correlation between the pollinating insects and distribution of flower types. It depends mainly on the dominant groups of local pollinators and on the stage of their sensory development which flower types prevail in a flora.

Some Conclusions

Taking the above described facts and findings under consideration, some conclusions can be deduced, as follows.

It is evident now that certain anthophilous insects have developed during their long sensory evolution a perfect order of special symbols and figure numerals as well, which they are able easily to remember and readily to distinguish from one another. As a result of an extensive selection, performed by pollinating insects, these symmetrical patterns became gradually fixed in definite flower types, where they continued to evolve parallel with the progressive sensory development of their pollinators. In keeping with the generally accepted terms, such as the "language" and "dances" of bees, the above described system might well be designated as an "alphabet" and "numeral system" of insects, in an allegoric sense. By mastering this "alphabet," a "litterate" let us say, insect is able to distinguish hundreds of plant species from one another, and to recognize its hidden food resources from a considerable distance.

This "alphabet" is not an assumption or theory, but rather a well-established system of directly observable patterns in nature. To master this "alphabet" means for anthophilous insects a not less important chance for survival than the command of "language" for social insects. As a matter of fact, all nectar deposits, which may vary in quantity and quality, as well as all pollen stores in flowers are marked with one of these symbols. In addition these symbols indicate how to reach nectar deposits that are hidden in stereomorphic and zygomorphic flowers, frequently behind long and labyrinthic passageways. Knowing a necessary number of these symbols, an "experienced" pollinator can easily orient himself among the multitude of food plants and estimate the food value and accessibility of every flower in advance. In this way he can save much time and energy that would otherwise be needed for examination of every single flower. It is safe to say that even a very slight saving of time and energy becomes in the aggregate of great importance for the survival of a species as a whole.

To the student of ecology and evolution, the deciphering of the "alphabet" of anthophilous insects is not less challenging than the lately discovered "sign language" of honeybees. It offers quite new opportunities to study the evolutionary relationship between plants and insects, and to comprehend in general the life and evolution in its higher levels during the age of angiosperms.

In this paper an attempt was made to parallel the floral differentiation of angiosperms with the sensory development of certain insect pollinators. This parallel-

ism is clearly reflected in the evolution of *semaphylls* (Leppik, 1956, p. 452), the showy parts of flowers designed for the *attraction of pollinating insects.* But there is much temptation also in the method of V. Grant (1950a) to study the evolution of *sporophylls,* particularly the development of an inferior ovary as a *protective device against devouring insects.*

In both these cases insects and flowers are mutually interrelated in evolution, as reciprocal selective factors. In this mutualism, however, two inverse ways of interaction are involved, as follows: a synagonistic and an antagonistic. *Synagonistic* mode of interaction results from a perfect *synagonism*[7] or cooperation of insects and plants, as consumers and producers. This cooperation is highly advantageous or even a necessity for the existence of both participants, providing thus an important precondition for a mutual adaptation of insects and plants to one another. An *antagonistic* trend, on the contrary, leads to the development of protective devices in plants against certain devouring insects. Since these insects tend to select for their meals flowers with less protected and more easily accessible ovaries, such selection has a reverse effect on plant evolution. But any antagonistic activity may turn over to synagonism as soon as such activity will have a mutual value and evolutionary significance for both participants, as in the case of *Pronuba yucasella.*

Summary

Systematic study and classification of flower types have revealed several observable trends in floral development. Morphologically graded series of recent flowers can be correlated with the general evolutionary trend of flowering plants. A further correlation between the evolution of flower types and the development of some sensory capabilities of pollinating insects is demonstrated by several concrete examples.

On the basis of these facts and findings a new view is emerging which sees in the food searching activity of pollinating insects an important selective factor which tends to keep the evolution of flowering plants in a predeterminated sequence. According to a recent theory, discussed in a previous report (Leppik, 1956), definite stages in the sensory development of pollinating insects must necessarily be reflected in corresponding levels in the evolution of flower types. In this paper, six distinguishable levels in the evolution of flower types are paralleled with the corresponding six stages of sensory development of pollinating insects, as shown in figures 2–3.

In addition, a presumptive sensory mechanism is discussed which obviously governs the food searching instincts of anthophilous insects and regulates their selective activity among flowers. Existence of such conjectural mechanism is adequately demonstrated in the orderly process of selection by these insects, which activity causes flower types to evolve in a certain, consecutive sequence. The aplication of this new theory will elucidate not only the historical development of a given flower type, but enables one to view also the further evolutionary tendency of present flower types. A practical yardstick for such evolutionary determinations is added for further criticism and possible use by students of evolution (fig. 2).

[7] *Synago* (συναγω) means to lead, drive, bring together. *Antagonism* (ανταγωνιζομαι) is opposition, counteraction, opposite meaning to *synagonism.*

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FERTILE HYBRIDS DERIVED FROM A WIDE SPECIES CROSS IN *ASTER*

CHARLOTTE J. AVERS

Department of Botany, University of Miami, Coral Gables, Florida

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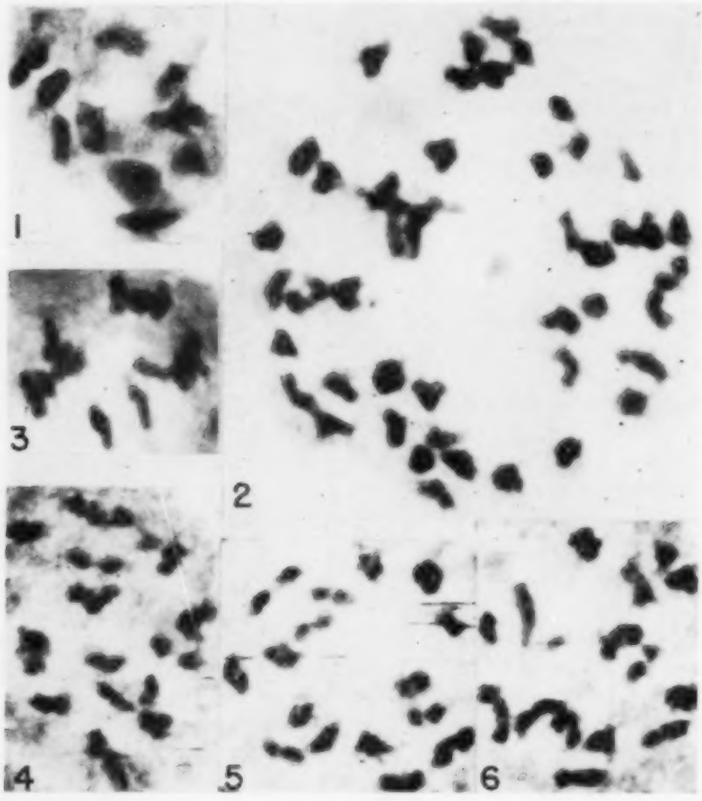
INTRODUCTION

Experimental crosses in *Aster* have yielded hybrids showing unusual chromosome behavior (Avers, 1954). Although occasional hybrids were produced, crosses between diploids and tetraploids were generally unsuccessful in the heterophyllous asters (Avers, 1953a). A number of diploid × tetraploid crosses yielded tetraploid hybrids, presumably due to the union of an unreduced egg from the diploid female parent with a reduced male gamete from the tetraploid parent. Reciprocal crosses in which the female parent was tetraploid and the male parent diploid were not successful. One interspecific cross did produce three triploid hybrids. In this cross of *A. cordifolius* ♀ ($2n$) × *A. shortii shortii* ♂ ($4n$) the triploid F_1 hybrids proved to be highly fertile despite meiotic irregularities (Avers, 1954). No backcross hybrids resulted when the triploids were crossed with the diploid *cordifolius* parent but many hybrids were obtained upon backcrossing to tetraploid *shortii*. These backcross hybrids were 90 per cent pollen-fertile although there were meiotic



FIGS. 1–6. Photomicrographs of PMC meiosis. × 1200.
1. *A. cordifolius*, $n = 9$
2. *A. turbinellus*, $n = 50$
3. F_1 *A. cordifolius* ♀ × *turbinellus* ♂, $n = 17$
4–6. F_2 *A. cordifolius* × *turbinellus*, $n = 17$.

irregularities and somatic chromosome numbers which varied from 33 to 35. Most of the crosses which were attempted showed that there was a high degree of chromosome homology among the species of Heterophylli (Avers, 1953a, b).

The present report concerns a wide species cross in which highly fertile F_1 and F_2 plants were obtained. The behavior and circumstances of this experimental hybridization were considered to be sufficiently interesting to justify the following account.

Materials and Methods

The two parent plants used in these crosses were obtained in different localities. The specimen of *A. turbinellus* Lindl. was sent by Dr. Edgar Anderson from St. Louis Co., Missouri, in 1950, and the *A. cordifolius* L. parent was collected by the author in Monroe Co., Indiana, in 1949. Reciprocal crosses were made in 1951 and two seeds were obtained from approximately two hundred pollinated florets. The technique of hybridization has been described previously (Avers, 1953a), and simply involved the contact of the heads of the parents for a period of one week, or until all the florets had matured and been pollinated. The heads were bagged between pollinations to prevent contamination. The pollen mother cells (PMC) were examined after staining with acetocarmine following preliminary fixation in chloroform-ethanol-acetic acid, 4 : 3 : 1. Pollen fertility was meas-

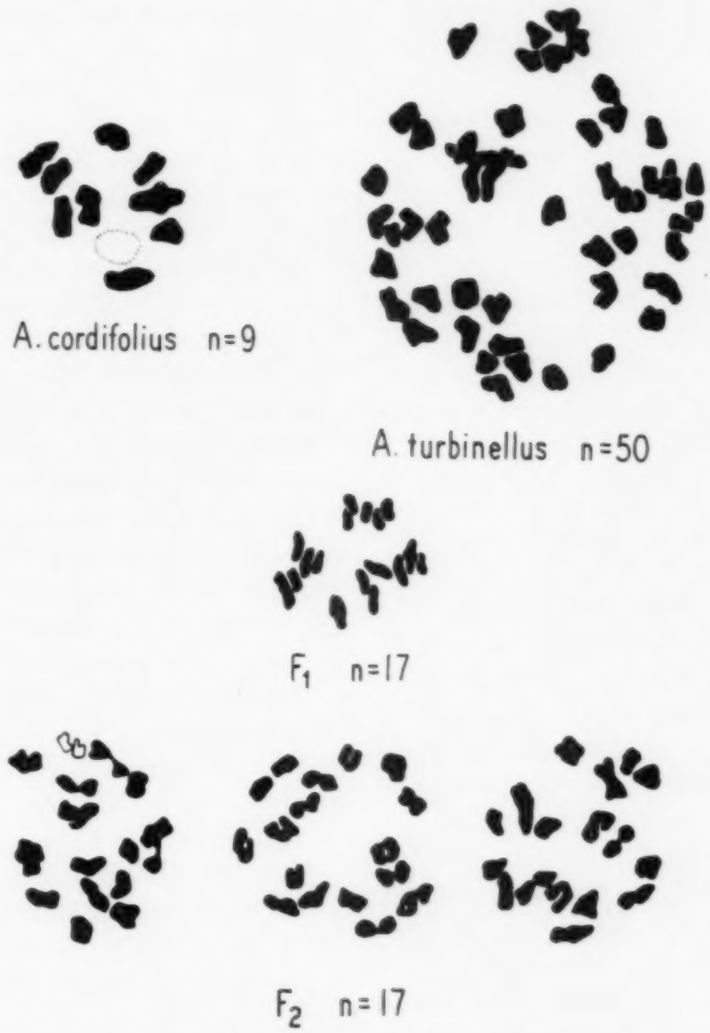
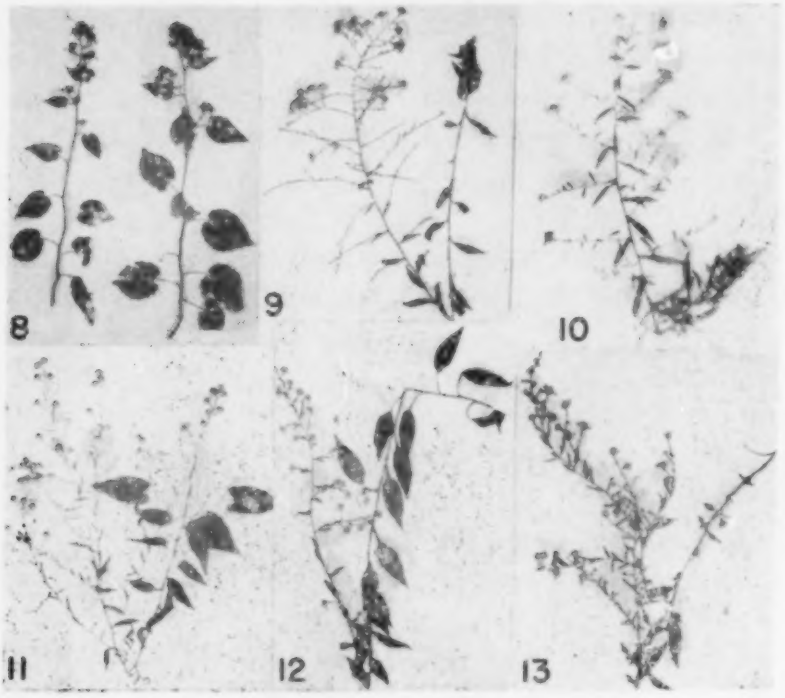


Fig. 7. Tracings of the photographs shown in figures 1–6.



FIGS. 8–13. Photographs of pressed specimens of experimental plants. × 1/6.

8. *A. cordifolius* parent
9. F_1 *A. cordifolius* ♀ × *turbinellus* ♂
10. *A. turbinellus* parent
11–13. F_2 *A. cordifolius* × *turbinellus.*

ured by relative stainability in cotton blue dissolved in lactophenol.

The seeds obtained from the *cordifolius* ♀ × *turbinellus* ♂ crosses were germinated after outdoor cold treatment of two months duration. The seedlings were grown in the greenhouse at Indiana University, as were all the plants involved in these experiments.

RESULTS

The two F_1 plants bloomed the first year and were quite vigorous. Their pollen fertility was 90–95 per cent, due in large part to the regular disjunction of 17 bivalents during meiosis. The chromosome number of the F_1 hybrids is doubly interesting if one considers the parental chromosome numbers. A cross between *A. cordifolius* ($n = 9$) and *A. turbinellus* ($n = 50$) should have yielded hybrids with a somatic chromosome number of 59, but only 34 chromosomes occurred in both F_1 plants.

The two F_1 hybrids were mutually pollinated in 1952 and 118 seeds were obtained from approximately 200 florets of one plant. The other F_1 plant set no seed at all. Fifty of these seeds were sown in 1953 and forty-five germinated to produce vigorous plants. All the plants involved were sent to Connecticut College and were grown there in the greenhouse until the present time. Cytological analyses were made of thirty of the F_2 generation and revealed $2n = 34$, with most of the PMC showing regularity of pairing and disjunction at meiosis. Occasional microsporocytes contained 16 bivalents and 2 univalents. These univalents behaved erratically at anaphase which contributed to the slightly reduced fertility in those plants in which they occurred.

Figures 1–6 are photomicrographs of representative PMC of the three generations of plants. Figure 7 is a chromosome diagram of the photographs shown in figures 1–6. Pressed specimens of parent and hybrid plants are shown in figures 8–13. The parents are quite distinct morphologically and the F_1 was intermediate in most characteristics. The three F_2 plants shown (figs. 11–13) indicate that the parental types were approached as early as the F_2 generation. The varia-

bility was high for all measured and observed taxonomic features.

Discussion

These results require that two main points be explained. First, the meiotic regularity in the hybrids, and second, the somatic chromosome number of 34 in the hybrids when 59 was expected. If we consider one possible basis for homology in the F_1 according to the following scheme:

$$P_1 \quad (n = 9) \quad A.\ cordifolius\ ♀ \times A.\ turbinellus\ ♂ \quad (n = 50)$$
$$\text{gametes} \qquad 9\,A \qquad \downarrow \qquad 9\,A, 16\,B$$
$$F_1\ (2n = 34)$$
$$(9\,A + 9\,A) + (8\,B + 8\,B) = 17 \text{ bivalents}$$

then it seems probable that meiotic regularity was due to auto- and allo-syndetic pairing of the chromosomes. This scheme implies a complex polyploid origin of *A. turbinellus*. This polyploid species must have at least one genome which is homologous with the *cordifolius* genome, otherwise univalents would have occurred during meiosis in the F_1. The eight remaining bivalents indicate that at least one genome of *turbinellus* has been duplicated. This genome probably is different from the *cordifolius* set since no multivalents were observed. Thus it seems that *A. turbinellus* contains a minimum of two distinct chromosome sets each of which has been duplicated once or twice. This is borne out further by the viability of *turbinellus* gametes which contained only 25 chromosomes instead of the usual 50. Impairment of viability would have occurred if the duplicated genomes had undergone divergent evolutionary changes. This also may indicate a relatively recent origin for *A. turbinellus*. There is abundant evidence of an $n = 9$ series in asters (Avers, 1953a; Darlington and Wylie, 1956) and the existence of an $n = 8$ series may be inferred from the studies of Clausen et al. (1940) on diploid and tetraploid *A. adscendens*.

Examples of autosyndetic pairing have been reported in hybrids from heteroploid crosses in *Prunus* (Darlington, 1930), *Papaver* (Ljungdahl, 1924) and *Crepis* (Collins et al., 1929). In crosses of *Papaver nudicaule* ($n = 7$) and *P. nudicaule* var. *striatocarpum* ($n = 35$) Ljungdahl reported that the F_1 hybrids were fertile and regularly showed 21 bivalents at meiosis. Backcrosses of the F_1 ($n = 21$) with *P. nudicaule* ($n = 7$) resulted in progeny with 14 bivalents at meiosis. In these crosses and in those involving polyploids of various genera, multivalent formation did not occur. Chromosomal homology was evident only in hybrids with reduced chromosome numbers, as may be the case in asters.

The second point involved here concerns the reduced number of chromosomes in the *turbinellus* gametes which contributed to the F_1. The PMC of *A. turbinellus* contained 50 bivalents, but the gametes which were successful in the crosses with *A. cordifolius* must have contained only 25 chromosomes as indicated in the crossing scheme. It is possible that somatic reduction occurred sometime prior to the development of the microspores. Other instances of somatic reduction have been reported (Menzel, 1950, 1952; Menzel and Brown, 1952). In the case of *A. turbinellus* it is not possible to determine the time of occurrence of somatic reduction. It is also likely that the reduced chromosome number arose in some other way, but it seems fruitless to speculate without additional evidence.

One other point is brought out by these results. It is not always possible to guess the probable ancestry of a polyploid. If the F_1 hybrids of *cordifolius* × *turbinellus* had been found in nature it seems unlikely that a correct interpretation of their ancestry would have been made. Most

likely a new basic chromosome number for *Aster* would have been announced since 17 is a prime number. This example may illustrate the pitfalls inherent in interpretations of polyploid origins based merely upon chromosome counts.

Summary

Results have been reported which strongly indicate a complex polyploid origin for *Aster turbinellus* ($n = 50$). Evidence was offered which suggested that there had been extensive duplication of the *turbinellus* genomes, one of which was apparently homologous with the 9-chromosome set of *A. cordifolius*. The expected number of 59 chromosomes did not occur in F_1 *cordifolius* ♀ × *turbinellus* ♂. Instead the F_1 hybrids contained 34 chromosomes which behaved regularly at meiosis. This was explained as the result of the pairing of one *A*-genome of *cordifolius* with an *A*-genome of *turbinellus* and autosyndetic pairing of two *B*-genomes of *turbinellus* to complete the 17 bivalents seen during meiosis. It was further suggested that somatic reduction preceded the formation of the *turbinellus* gametes involved in the hybridizations, which accounted for the lowered F_1 chromosome number. The F_2 generation was also highly fertile and contained a somatic chromosome number of 34.

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CORRECTION

Figure captions for "Rate of Development of Viability Mutants in *Drosophila melanogaster*," Gert Bonnier and Ulla B. Jonsson and for "Cy L Versus Cy L-Pm Technique in *Drosophila melanogaster*" Gert Bonnier, Volume XI, Number 3, September, 1957, are incorrect. The caption for figure 1 of the former, page 272, is printed under figure 1 of the latter, page 370. The caption entered on page 272 is in error. The caption for figure 1 of the article "Cy L Versus Cy L-Pm Technique in *Drosophila melanogaster*" should read as follows:

FIG. 1. Diagram showing the difference between the Cy L- and the Cy L-Pm techniques. P_1 wild type males are mated singly to females from a Cy L/Pm stock; In F_1 Cy L or Pm males are again mated singly to females from a Cy L/Pm stock; in F_2 the Cy L/+ females are according to the Cy L-technique mated to Cy L/+ males, but, according to the Cy L-Pm technique mated to Pm/+ males. The survival rates are calculated from the F_2 counts.

ANNOUNCEMENTS

The Ninth International Botanical Congress will be held in Montreal, Canada, from August 19 to 29, 1959, at McGill University and the University of Montreal. The program will include papers and symposia related to all branches of pure and applied botany. A first circular giving information on program, accommodation, excursions, and other detail will be available early in 1958. This circular and subsequent circulars including application forms will be sent only to those who write to the Secretary-General asking to be placed on the Congress mailing list:

DR. C. FRANKTON
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IX International Botanical Congress
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The Division of Biological and Medical Sciences of the National Science Foundation announces that the next closing date for receipt of research proposals in the life sciences is January 15, 1958. Proposals received prior to that date will be reviewed at the Winter meetings of the Foundation's Advisory panels and disposition will be made approximately four months following the closing date. Proposals received after the January 15, 1958, closing date will be reviewed following the Spring closing date of May 15, 1958.

In addition to funds for the support of basic research in the life sciences, limited funds will be available during the current fiscal year for the support of research facilities and programs at biological field stations.

Inquiries should be addressed to National Science Foundation, Washington 25, D. C.

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